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Living foraminiferal assemblages in two submarine canyons (Polcevera and Bisagno) of the Ligurian basin (Mediterranean Sea)

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ABSTRACT

Living (Rose-Bengal stained) benthic foraminifera were investigated in eleven stations sampled along transects following a depth gradient from Polcevera and Bisagno canyons and the adjacent open slope (Ligurian Sea), in a depth interval ranging from 200 to 2000 m. In order to understand which environmental factors influence the abundance and taxonomical composition of the foraminiferal assemblages in these two domains (canyon and open slope), qualitative and quantitative foraminiferal data were correlated to the sediment biochemical composition (in terms of phytopigments, proteins, lipids, carbohydrates and biopolymeric carbon), grain size and the main hydrological characteristics (salinity, temperature, dissolved oxygen). The Cluster Analysis and Canonical Correspondence Analysis allowed us to detect two sectors (coastal and offshore) characterized by contrasting trophic conditions. The coastal sector reflects spread meso-eutrophic conditions in both physiographic domains being possibly more impacted by the river inputs and sediment transport processes from land. In fact, the narrow continental shelf of the Ligurian Sea favors the deposition of sediment transported by riverine processes on the immediately adjacent coastal areas. As a result homogenization of sea-bottom conditions occurs, leading to an unclear differentiation between open slope and canyon foraminiferal assemblages. Conversely, the offshore sector is less affected by physical disturbance due to the sedimentary flows decreasing in relation to the larger distance from the coastline. Consequently, the lower organic matter content and lower food quality (expressed in terms of contribution of the primary material to the biopolymeric carbon pool) lead to a more oligotrophic condition, which favors the development of peculiar assemblages dominated by *Glomospira charoides*, *Ammolagena clavata* and epifaunal taxa. The first finding ever of a warm tropical species (*Amphistegina lessonii*) in the Ligurian Sea sediments at 500-m depth can be considered the first evidence of upward expansion of tropical species to the Northern portion of the Mediterranean Sea, which is experiencing an evident water warming linked to the ongoing global climate change.

1. Introduction

Submarine canyons are complex and common systems around the continental margins (Harris and Whiteway, 2011) that are characterized by an interplay between hydro-sedimentary and biological process (Canals et al., 2006, 2009; Duros et al., 2014). Due to their steep morphology, can receive high amount of organic matter seasonally and show enhanced detrital accumulation by channeling and trapping coastally derived material (Shepard and Dill, 1966; Canals et al., 2006). These pulse-like processes involve complicated hydrodynamic patterns that contribute to increase habitat heterogeneity and enhance productivity along continental and oceanic island margins (Rowe et al., 1982; Vetter et al., 2010). Intense and irregular sedimentary dynamics, consisting of down-slope transport of material, associated turbidity currents, cascading of dense shelf water behaving as flushing conduits, and scouring of the seafloor, can disturb the benthic communities but, at the same time, can create habitats for new faunal colonization (Nardelli et al., 2018; Pierdomenico et al., 2019). Moreover, dissolved and particulate terrestrial material from the continental shelf play an important role in increasing both pelagic and benthic productivity (Lohrenz et al., 1990, 1997; Vetter and Dayton, 1999; Dagg and Breed, 2003; Goineau et al., 2011). In fact, the increased food availability

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related to the organic material accumulation in submarine canyon sediments can favor the development of different benthic assemblages which benefit from the enhanced influx of organic matter (van Oevelen et al., 2011; Pierdomenico et al., 2017).

Foraminifera are an important, an often numerically dominant, component of benthic communities. They are protists, that in deep-sea sediments even make up to 80% of the faunal biomass (Snider et al., 1984; Van der Zwaan et al., 1999). Their distribution is controlled by several physical, chemical and biological factors and they play an important role on the food chain and in biogeochemical cycles (Van der Zwaan et al., 1999). Foraminifera are recognized as excellent indicators of past and modern environmental conditions (Alve, 1995; Murray, 2001, 2006; Sen Gupta, 2002; Schönfeld et al., 2012). Recent studies demonstrated that the analyses of living assemblages allow to achieve useful information regarding the environmental characteristics (physico-chemical) of the seafloor. Furthermore, faunal abundance, diversity and species composition can be used to provide integrated insights into the spatial and temporal changes in the environmental conditions (e.g. Jorissen, 1988; Schönfeld, 2002; Scott et al., 2005; Murray, 2006; Koho et al., 2007; Fontanier et al., 2008; Duros et al., 2014; Di Bella et al., 2016). Previous studies carried out on living foraminiferal assemblages in submarine canyons, were mainly focused on the western Atlantic margin (e.g. Nardelli et al., 2010; Koho et al., 2007; Duros et al., 2014) or the NW Mediterranean sector (Schmiedl et al., 2000; Fontanier et al., 2008; Goineau et al., 2011; Contreras-Rosales et al., 2012; Bolliet et al., 2014). Recently, Di Bella et al. (2017) studied an active submarine canyon located in the Southern Tyrrhenian margin (central Mediterranean Sea). In this area, sedimentary processes are linked to a complex physiographic and geological setting that encompasses a very narrow continental shelf and strong seasonal discharging due to high-energy and ephemeral streams locally called "*fiumare*" similarly to the setting of the Ligurian margin. These studies suggest that the foraminiferal distribution is greatly influenced by specific ecological conditions within canyons, related to turbidity current activity and/or organic carbon fluxes (Schmiedl et al., 2000; Fontanier et al., 2005; Hess et al., 2005; Di Bella et al., 2017). Particularly, the benthic foraminiferal distribution is strongly influenced by the organic carbon flux rates and by the quantity and quality of organic matter (e.g. Van der Zwaan, 1982; Gooday, 1988; Altenbach and Sarnthein, 1989; Loubere et al., 1993; Fariduddin and Loubere, 1997; Rathburn and Corliss, 1994; De Rijk et al., 2000; Hess and Jorissen, 2009; Nardelli et al., 2010). The availability of food is strictly related to the hydrodynamic conditions and the current strength (Altenbach and Sarnthein, 1989; Hess and Jorissen, 2009); moreover, the geomorphological and hydrodynamic characteristics of the continental margins, such as the presence of river mouths, can greatly influence the development of oligotrophic and/or eutrophic conditions at the bottom and along the entire water column (Nezlin et al., 2004; Kaiser et al., 2014).

The complex interplay of all these factors influences differently the foraminiferal distribution. It has been observed that in some cases (e.g. Whittard Canyon, NE Atlantic) foraminiferal assemblages varied with water depth, but they are also different between canyon branches and adjacent slopes (Duros et al., 2011). Conversely, in other cases (e.g. Cap de Creus Canyon), no clear differences were evidenced in the compositional fauna between the two domains (canyons and adjacent slopes), especially at deeper depths (Swallow and Culver, 1999; Contreras-Rosales et al., 2012). Nardelli et al., 2018, in the same area, evidenced the influence of episodic disturbance events (i.e., dense shelf water cascading (DSWC) and open-ocean convection (OOC)) on the living foraminiferal assemblages which changed considerably in comparison to those reported by Contreras-Rosales et al., 2012 and a different foraminiferal distribution between 1000 m depth stations and deeper depths.

The BioLig (Biodiversity, ecosystem functioning and pelagic-benthic coupling in Ligurian submarine canyons) cruise carried out from 30th April to 20th May 2013, provided us the opportunity to investigate two submarine canyons (Polcevera and Bisagno) in the Gulf of Genoa, Ligurian Sea (western Mediterranean Sea). This research represents a contribution to understand the complex mechanisms that interplay to control the foraminiferal benthic communities in peculiar physiographical and geological settings (narrow continental shelf, strong seasonal discharging due to high-energy and ephemeral streams), characterizing some sectors of the western Mediterranean basin. The aim of the present study is to investigate the living benthic foraminiferal assemblages (soft and hard-shelled taxa) from the two canyons and the adjacent open slope, and to identify the main drivers controlling their distribution. To address these goals, we adopted a multi-proxy approach including foraminiferal, biogeochemical and sedimentological data. We investigated faunal abundance, assemblage composition, species diversity together with quantity and biochemical composition of organic matter (in terms of phytopigment, protein, lipid, carbohydrate content) along a depth gradient (from 200 to 2000 m) in the two environmental domains (the canyon axes and the adjacent slope).

2. Geological and oceanographic setting

The Gulf of Genoa is located in the northern part of the Ligurian Sea (northwestern Mediterranean Sea, Fig. 1). The Ligurian basin shows the typical features of a tectonically active margin with seismic activity: a high slope gradient and steep submarine canyons fed by short mountain supplied rivers, highly affected by severe landsliding processes also favored by the presence of a mobile evaporitic layer (salt), potential dissociation of gas hydrates and effect of hyperpycnal flows triggered by riverine inputs (Migeon et al., 2011 and references therein). The steep Ligurian margin is incised by numerous canyons that follow the direction of the main faults that characterize the Alpine and Ligurian regions (Chaumillon et al., 1994; Larroque et al., 2001). Among these canyons, the Polcevera and Bisagno are located in the central part of the gulf. These canyons are the submarine extension of the Genoa hinterland rivers and initiate directly at the mouth of these rivers feeding the Ligurian basin on the upper continental slope. All canyons merge at about 2000 m water depth into a larger submarine valley called Genova Submarine Valley (Migeon et al., 2011). Slope instability affects all the Ligurian margin either in the areas surrounding the mouth of the mountain-supplied rivers at shallow water depth (< 200 m) or at the base of the continental slope, between 1700 and 2200 m of water depth (Migeon et al., 2011) causing submarine landslides that strongly impact the benthic ecosystem.

The oceanographic setting is dominated by a cyclonic circulation system fed by the East Corsica Current (ECC) and the West Corsica Current (WCC) known as the Ligurian Provencal Catalan Current (LPCC) flowing along the continental slope (Astraldi et al., 1995; Millot, 1991; Kaiser et al., 2014). These cyclonic circulation produces a zone of divergence that determines a cold and nutrient-rich water drawing toward the upper mixed layer in the central part of the Ligurian Sea (mean SST 17 °C), and downwelling of the water masses in the peripheral zone (mean SST 18 °C) (Millot, 1999; Nezlin et al., 2004). As a result, a frontal system separates the cold and dense water of the central part of the basin from the warm and light water from shelf/slope LPPC flowing around it (Nezlin et al., 2004). This circulation pattern implies that the Ligurian Sea is colder than the Tyrrhenian Sea, determining differences in the composition and physiognomy of their respective marine biota. The basin is characterized by a progressive deepening of the thermocline in winter and water stratification in spring. The Ligurian Sea is classified as an oligotrophic basin (Nezlin et al., 2004; D'Ortenzio and Ribera d'Alcalà, 2009). In the southwestern part of the Ligurian Sea (e.g. Bosc et al., 2004), surface layers with inorganic nutrients come from the Levantine Intermediate Water (e.g. Savenkoff et al., 1993). The primary production consists of seasonal algal blooms (spring and autumn) and oligotrophic conditions in summer. Moreover, coastal waters are characterized by an intense hydrological

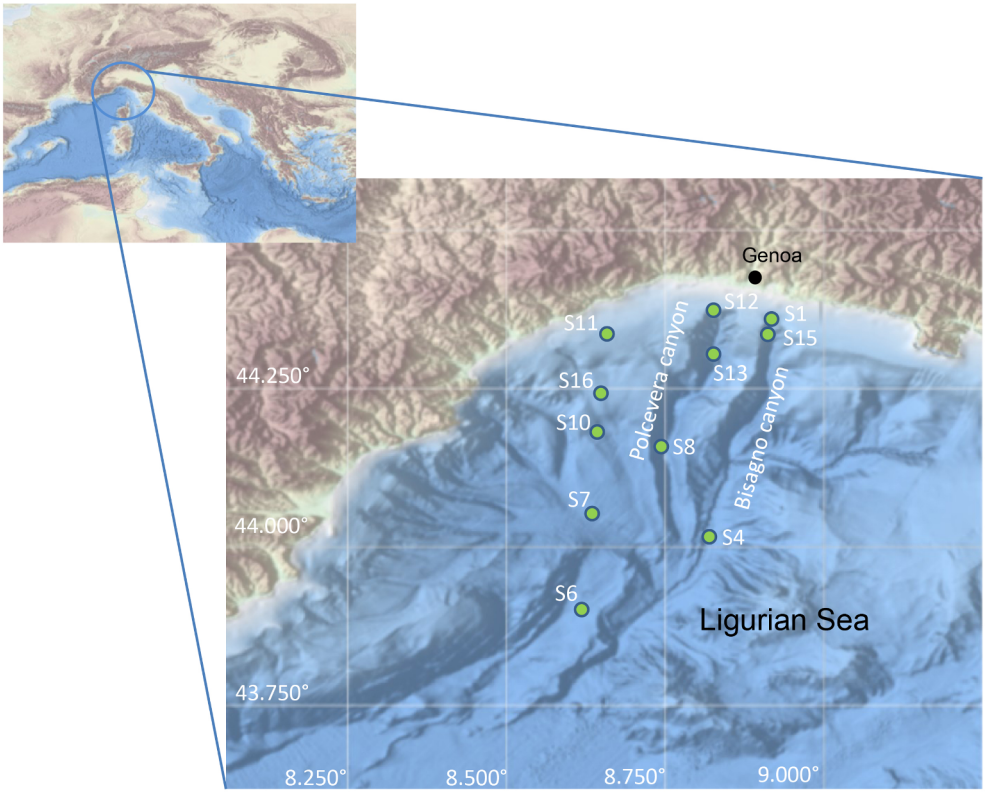


Fig. 1. Location of the studied stations in the Ligurian Sea (NW Mediterranean Sea). The image has been created through the bathymetry web portal http://portal.emodnet-bathymetry.eu/. Latitude coordinates are in °N; longitude coordinates are in °E. The black dot is the position of the city of Genoa.

heterogeneity due to local eddies that can generate upwelled nutrients inside the basin and in its marginal rim (Casella et al., 2011). In the study area, most of the organic matter input appears to be concentrated in front of the Bisagno and Polcevera rivers, and these tributaries are believed to represent the main source of nutrients that sustains the primary production in the coastal area (Lazzara et al., 2010; Kaiser et al., 2014).

3. Materials and methods

3.1. Sampling area and strategy

Surface sediment samples were collected during the BioLig cruise carried out from 30th April to 20th May 2013 on board of the Italian R/V Minerva Uno, in the Ligurian Sea.

Two different physiographic domains, canyons and adjacent open slopes, were studied in order to highlight environmental conditions characterizing each sector. A total of eleven stations were sampled by using a NIOZ-type box-corer (which prevents sediment washing during the retrieval, and allow the collection of undisturbed sediment samples; Danovaro, 2010). For the analysis of benthic foraminifera, grain size and organic matter analysis (Fig. 1; Table 1), 5 stations were sampled along the slope and 6 stations within the Polcevera and Bisagno canyons, at depth intervals ranging from 200 to 2000 m.

Grain size analyses were conducted by sieving on mesh nets (Covazzi et al., 2019). At all stations, data on water column characteristics (pressure, salinity, conductivity, temperature, dissolved oxygen concentration and fluorescence) were measured with a CTD-Rosette system, consisting of a CTD SBE911 plus, during the same cruise (Celussi et al., 2018).

3.2. Quantity and biochemical composition of sedimentary organic matter

The analyses were carried out as described in more detail in Pusceddu et al. (2014). Briefly, chlorophyll-a and phaeopigment analyses were carried out according to Lorenzen and Jeffrey (1980). Pigments were extracted from sediments by using 90% acetone (for 12 h in the dark at 4 °C) and analyzed fluorometrically to quantify chlorophyll-a concentration and, after acidification with 0.1 N HCl, to estimate the amount of phaeopigments. Total phytopigments (expressed as the sum of chlorophyll-a and phaeopigments) were converted into carbon equivalents by using the conversion factor of 40 μg of C μg^{-1} (Pusceddu et al., 2009; Danovaro, 2010) and used to estimate the organic material of algal origin, including the living (chlorophyll-a) and senescent/detrital (phaeopigment) fractions (Danovaro, 2010). The contents of proteins, carbohydrates and lipids in the sediments were determined spectrophotometrically (Danovaro, 2010). Protein concentration was obtained according to the procedure by Hartree (1972) and reported as mg albumin equivalents per dry weight g of sediment. Carbohydrates were analyzed according to Gerchakov and Hachter (1972) and expressed as mg glucose equivalents per dry weight g of sediment. Lipids were extracted with methanol and chloroform (2:1 vol/vol) (Danovaro, 2009), and lipid concentrations reported as mg tripalmitine equivalents per dry weight g of sediment. Protein, carbohydrate and lipid concentrations were converted into C equivalents by using the following conversion factors: 0.49, 0.40 and 0.75 μg C μg^{-1}, respectively (Fabiano et al., 1995), and their sum referred to as biopolymeric C (BPC). The fraction of BPC represented by relatively fresh algal material was also assessed as the percentage contribution of phytopigment C to BPC content, and referred to as the algal fraction of BPC. For all biochemical assays, blanks were obtained using pre-combusted sediments (450 °C for 4 h).

3.3. Foraminiferal analyses

At each station, sediment cores were sub-sampled for foraminifera from each box-corer using plexiglas tubes, that were carefully pushed into the sediment profile to prevent disturbance. The cores were then

Table 1
Location of the sampled stations with sampling depth, geographic coordinates and data of temperature T (°C), dissolved oxygen DO (ml/l) and salinity (psu) measured at the bottom. All data are from the Biolig Report (2013), and Celussi et al. (2018) with the exception of grainsize data which are from Covazzi et al. (2019).

Station	Depth (wd) m	Latitude (N)	Longitude (E)	T	DO	Salinity	Gravel (%)	Sand (%)	Silt (%)	Clay (%)
Canyon										
S1	226	44° 21′07.8138″	08° 54′ 44.8260″	13.5	4.8	38.347	0	4.39	55.31	40.3
S15	496	44° 20′ 07.0032″	08° 54′ 38.0784″	13.4	3.5	38.559	2.02	5.61	52.37	40
S4	1945	44° 00′ 41.2956″	08° 49′ 05.6676″	13.2	4.1	38.479	0	1.61	53.39	45
S12	253	44° 21′ 52′3032	08° 49′ 19.5666″	13.5	4.1	38.392	0	0.99	57.81	41.2
S13	1001	44° 18′ 43.1392″	08° 49′ 52.6998″	13.3	4.7	38.530	0	5.73	53.17	41.1
S8	1620	44° 10′ 35.0634″	08° 45′ 42.5256″	13.1	3.9	38.479	0	0.76	50.24	49
Slope										
S11	225	44° 18′ 47.1036″	08° 40′ 13.6722″	13.5	3.9	38.410	0	2.17	60.73	37.1
S16	509	44° 16′ 12.7848″	08° 40′ 17.6532″	13.4	4.0	38.554	0	0.82	55.58	43.6
S10	1055	44° 11′ 22.4316″	08° 40′ 31.0470	13.2	4.2	38.524	0	0.78	57.12	42.1
S7	1516	44° 03′ 24.2676″	08° 39′ 09.2184″	13.2	4.0	38.484	0	0.73	51.57	47.7
S6	2004	43°55′ 01.9546″	08° 38′ 10.0365	13.2	4.6	38.480	0	4.22	51.48	44.3

sliced collecting 0.5 cm-thick subsamples from the top to 2 cm of depth, and 1 cm thick subsamples from 2 cm to 5 cm depth along the core. Foraminiferal literature data (e.g. Gooday, 1988; Kitazato et al., 2000; Heinz and Hemleben, 2003; Nardelli et al., 2010, Di Bella et al., 2017) show that in the deep environments, the topmost sediment layers contain generally about 90% of the total assemblages. For this reason the study was limited to the topmost 5 cm.

We followed the standard procedure to study hard- and soft-celled specimens (Sabbatini et al., 2012). To distinguish the living fauna, the sediment samples were stained and preserved in a solution of 90% ethanol with 2 g/l of Rose Bengal as described by Walton (1952), Lutze and Altenbach (1991), Schönfeld et al. (2012). After 15 days, the samples were wet-sieved through a 63 μm sieve and then dried at 40 °C. In each sample, Rose Bengal stained foraminifera with well-preserved tests were considered. Non-transparent agglutinated and porcelaneous tests were broken in order to inspect the interior. In many samples, tubular fragments (about 200μ −1cm) belonging to different agglutinated tests (genera: *Rizhammina Rhabdammina*, *Hyperammina*), were found. To prevent abundance over-estimate of these tests, only specimens at least 0.5 cm in length were counted.

Some parameters such as faunal density and diversity indices were considered in order to investigate on the structure of the foraminiferal community at the sediment water interface and within the sediment. Living (stained) faunal abundance was normalized to a standard volume of 50 cm^3. Species diversity was quantified considering the number of taxa occurred in the samples that is species richness (S). However, S does not consider the species abundance and is highly sensitive to sample size (Fontanier et al., 2014); therefore, the Shannon-Weaver (H) and Eveness (E) indeces were also calculated using the PAST 3.18 (PAlaeontological STatistics) data analysis package (Hammer et al., 2001).

In order to investigate the foraminiferal vertical distribution, we calculated the Average Living Depth (ALD_x) for the total fauna in the first 5 cm of the sediments as follows (Jorissen et al., 1995):

$$ALD_x = \sum_{i=1,x} (n_i \times D_i)/N$$

in which ALD_X is the average living depth (cm) of the fauna in a core of x centimeters depth; n_i is the number of specimens in the sediment interval i; D_i is the midpoint of the sediment interval i (cm); and N is the total number of individuals for all levels. The foraminiferal density histograms (single species abundance in each sediment layer was normalized to a standard volume of 50 cm^3) at each station are shown. For each sample, all benthic living well-preserved specimens were picked, counted and identified according to the generic classification of Loeblich and Tappan (1987). The species identifications were mainly based on previous studies of shelf and canyon systems in Mediterranean and extra-Mediterranean basins (Cimerman and Langer, 1991; Sgarrella and Moncharmont-Zei, 1993; Koho et al., 2007; Sen Gupta et al., 2009; Milker and Schmiedl, 2012).

Digital photographs of the most significant taxa and Energy Dispersive Spectroscopy

(EDS) analysis were obtained using a scanning electron microscope (FEI QUANTA 400) at the SEM Laboratory of Earth Sciences Department – Sapienza University of Rome (Italy).

3.4. Statistical analyses

Statistical analyses were carried out using Primer v6 software (Clarke and Gorley, 2006) using a simplified matrix of species abundance occurring in the sediment interval of 0–5, where only those species showing abundances greater than 1% in at least one station were considered (Patterson and Fishbein, 1989; Fishbein and Patterson, 1993). To identify the benthic foraminiferal assemblages occurring in the study area, a Hierarchical Cluster Analysis (HCA) with group-averaged linkage was performed, using a Bray–Curtis similarity matrix derived from square root transformation of species abundance data. The similarity percentage (SIMPER) routine was then applied to the resemblance matrix to identify the species characterizing the assemblages and to determine, by means of pair-wise comparisons, the species contributing most to dissimilarity between assemblages. Non-metric multidimensional scaling (MDS) was also applied to the resemblance matrix to order the stations in a two-dimensional plot, to visually assess the similarities among the stations. The significance of groups segregation obtained from the HCA was tested by ANOSIM analysis (ρ-value ≤ 0.001 was considered as significant).

Moreover, Canonical Correspondence Analysis (CCA) was used to highlight the effects of the environmental gradient from canyon to open slope and from coastal to deep sites. CCA is considered one of the best tools for ecological studies, in which matrices containing species abundance are processed to uncover factors determining community structure (Palmer, 1993). For this analysis, in order to simplify the matrix, the relative abundance of taxa greater than 10% in at least one station were considered, together with environmental variables including depth, water masses characteristics (temperature, dissolved oxygen and salinity measured at the bottom) and biochemical content in the sediments (expressed as total lipids, carbohydrates, phytopiments and proteins) (Appendix A).

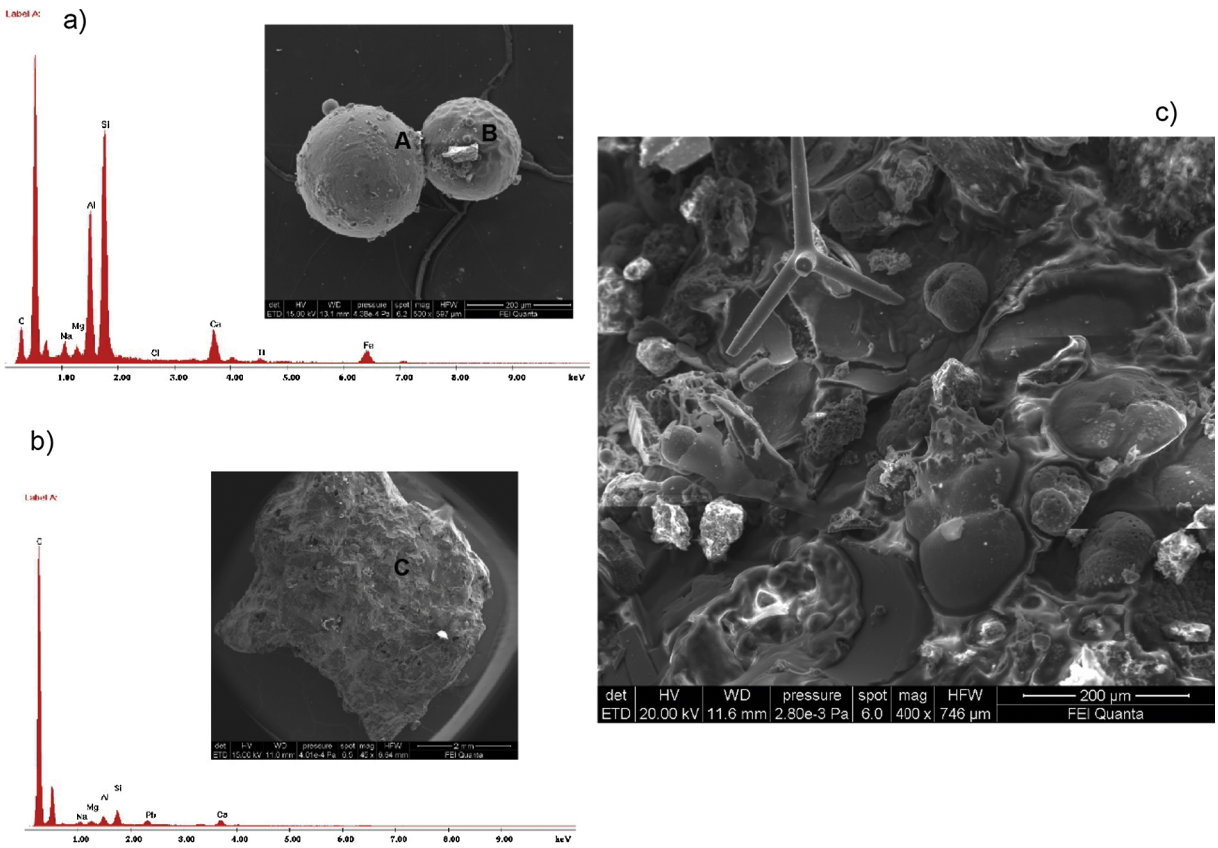


Fig. 2. SEM micrographs showing presence of anthropogenic material in the sediment samples: (a) S4, spherules related to industrial products; (b) S10, oil derivative products; (c) S4, Foraminifers and sponge spicules sunk in tar material. In (a) and (b) the EDS analysis performed on A, B and C spot points are also shown.

4. Results

4.1. Environmental setting

The sediment samples mainly consist of silty clay (Table 1). In more detail, the silt content ranges from 50.2 to 60.7% and the highest values are recorded at the open slope sites between 200 and 1000 m depth (S11-S10). At the canyon head (S1, S13, S15) the samples contain the highest percentage of sand (values ranging between 4 and 5%). Similar values (4.2%) of sand are observed at the deep site S6. The clay content ranges from 37 to 49% with the maximum values at the deeper stations both in canyon and open slope sites. Gravel (2%) occurs only at 500 m (S15) in the Bisagno canyon head. Moreover, in most of the samples, micromaterial of anthropogenic origin and coal tar are recorded (Fig. 2).

As regards the water masses observed during the cruise, most of the sampled stations are affected by the presence of Levantine Intermediate Water (LIW, 300–1000 depth) as evidenced by the high salinity and the oxygen minimum values. In several stations, LIW extends down to the bottom. The Western Mediterranean Deep Water (WMDW) is detectable only in the deepest stations (S4, S6). The main seawater parameters recorded both in the canyon and slope sites, show rather constant values: temperature varies from 13.1 to 13.5 °C, salinity ranges from 38.35 to 38.56, while dissolved oxygen displays values from 3.5 to 4.8 ml/l (Celussi et al., 2018). The thermocline and halocline configuration are generally of “cyclonic type”, indicating a surface westward geostrophic flow, in accordance with the Ligurian Current.

4.2. Organic matter biochemical composition

Total phytopigment concentrations range from 0.1 to 0.6 µg g^{-1} for chlorophyll-a and from 2.4 to 24.4 µg g^{-1} for phaeopigments (Appendix A). The highest concentrations are observed in the Bisagno and in the Polcevera canyons at 496 m (S15) and 252 m (S12) depth respectively. With the exception of the values observed at 225 m (S11) depth in the open slope, the concentrations of phytopigments are significantly higher in the canyons than in the open slope sites located at comparable depths (Fig. 3a). The carbohydrate carbon represents the major fraction of biopolymeric C accounting > 40% of the total biopolymeric matter pool followed by proteins (ca 40%) and lipids (typically less than 20%) (Fig. 3b,c). The biochemical composition of sedimentary organic matter significantly varies between canyons and slope at 200, 500 and 1000 m depth and between all depths sampled along the two canyon axes and adjacent slope. Both in the slope and canyons we observed significant increase in the percentage contribution of carbohydrates to total organic matter with increasing water depth.

The concentration of biopolymeric C (Fig. 3b) is higher in the canyons than in the open slope, with significantly higher values registered at 200 m (in both canyons) and 500 m depth (in the Bisagno canyon) compared to the adjacent slope. The highest values are found at 226–252 m depth (S1-S12) in the Bisagno and Polcevera canyons (2.7 and 2.5 mgC g^{-1}, respectively (Appendix A). The contribution of phytopigments to the biopolymeric carbon is significantly higher in the two canyons than in the open slope at all sampling depths, except for 200 m depth. The autotrophic fraction of the organic matter pool reaches almost 50% at 496 m depth (S15) in the Bisagno canyon. The lowest contribution is observed at 2004 m depth (S6) in the open slope.

4.3. Foraminiferal assemblages

The total standing stocks (TSS) of living foraminifera are reported in Table 2, while their vertical distribution along sediment profile is shown in Fig. 4. As a general feature, the assemblage structure parameters decrease with increasing water depth. The highest values are

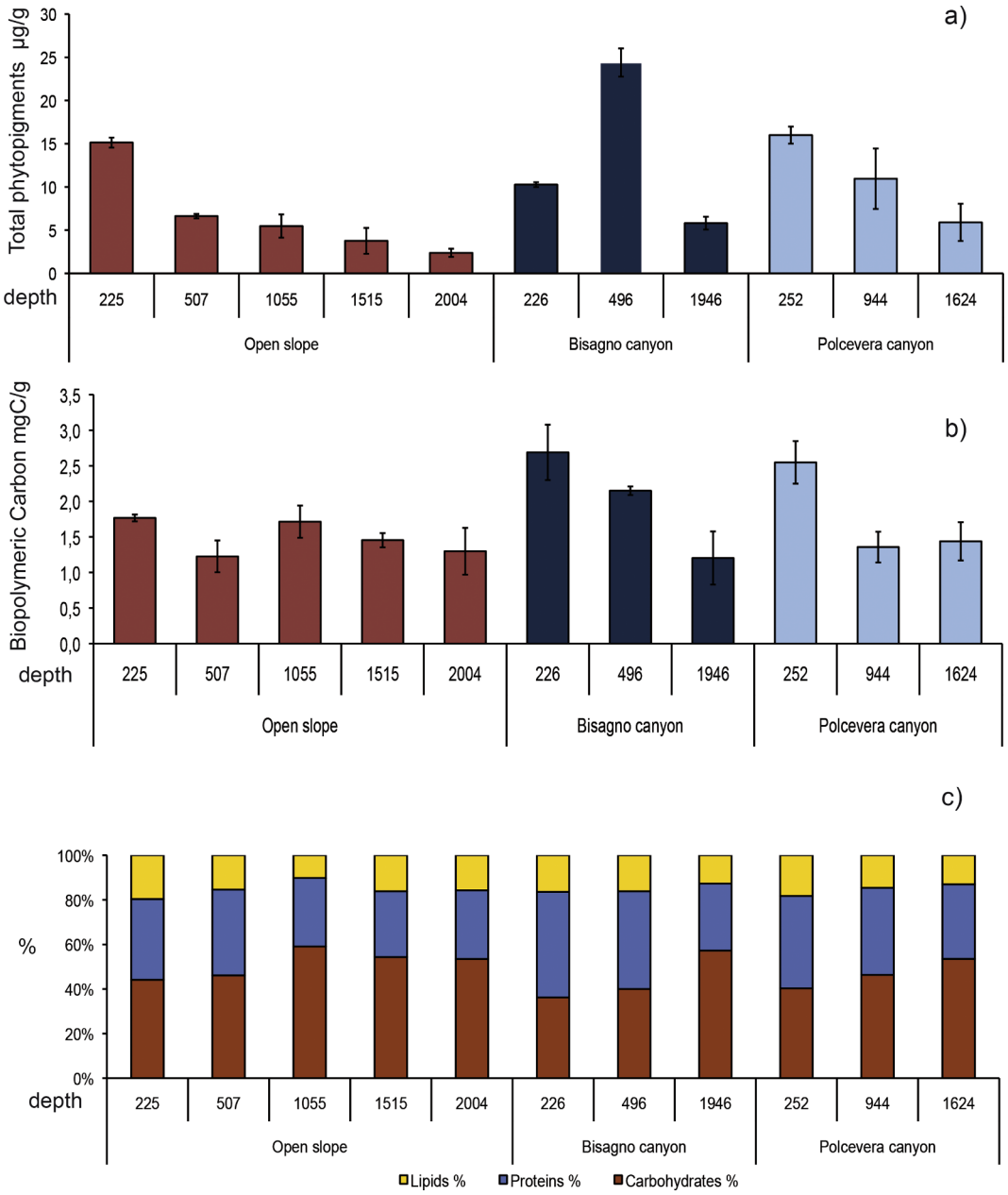


Fig. 3. Concentration of organic matter and its biochemical composition in the investigated area. Reported are: phytopigment concentrations (a), biopolymeric C concentrations (b) and relative contribution of carbohydrates, lipids and proteins to the biopolymeric pools (c).

recorded at S15 in the Bisagno canyon at 500 m water depth (164 individuals) and at S11, in the slope, at 200 m water depth (150 individuals). On average, the canyon stations display higher TSS values than those from the slope, showing a decreasing trend with the increase of depth, except for the S1 that (at the head of the Bisagno canyon, 200 m depth) that records only 89 individuals. Conversely, at the slope stations the TSS distribution appears more variable: at about 200 m depth (S11) the TSS values are similar to the Polcevera site at the same depth (S12), between 500 m (S16) and 1000 m (S10) the faunal density abruptly decreases (Fig. 4) while it successively increases again to 2000 m depth (S7, S6).

Species richness (S) generally decreases with the increasing depth in both domains (canyons and open slope), analogously to the Shannon index H. The foraminiferal assemblage at station S15 (500 m) in the Bisagno canyon, exhibits the highest values of TSS, S and H (Table 2).

As for the foraminiferal test composition, differences can be drawn in the different physiographic domains (Fig. 5). A total of 51 hyaline, 17 porcelaneous, 25 agglutinated and 2 soft-walled taxa are recognized. Hyaline tests dominate all sites except for S4 (1945 m, Bisagno canyon) and S10 (1000 m, slope) where agglutinated taxa constitute the most abundant group. It is worthy to note that agglutinated taxa increase with depth in both domains: in the canyon sites and in the open slope, they significantly increase from about 1000 m, and from 500 m depth respectively. The porcelaneous taxa are very scarce at all stations with frequencies < 9% (mainly *Quinqueloculina* spp., *Biloculinella depressa*, *Sigmoilopsis celata*, *Spiroloculina excavata*, *Pyrgo* spp.), while at S10 station they are totally absent. The soft-walled taxa are poorly represented everywhere across the study area. They are recorded only in the deepest stations (S6 and S7) of the slope with morphotypes belonging to genera *Nodellum* and *Hospitella*.

4.3.1. *Vertical distribution of living foraminifera*

The vertical distribution of foraminifera in the sediment for each station is shown in Fig. 6 (Bisagno and Polcevera canyons) and Fig. 7

Table 2
Summary of the living foraminiferal data in each station. TSS: Total Standing Stock standardized to 50 cc; n/50 cc: living (stained) specimens abundance normalized to a volume of 50 cm^3; ALD5(cm): Average Living Depth for the total fauna in the first 5 cm; S: number of taxa; H: Shannon index; E: Eveness; Hyaline, Porcelanaeous, Agglutinated and Soft-walled specimens.

Station	Depth (wd) m	TSS_{50cc}	n/50 cc	ALD_5 (cm)	S	H	E	Hyaline	Porcel.	Agglut.	Soft-walled
Canyon											
Bisagno S1	226	89	1.78	2.81	31	2.04	0.87	244	25	9	0
Bisagno S15	496	164	3.28	1.36	51	2.43	0.83	372	50	91	0
Bisagno S4	1945	135	2.70	1.01	11	1.15	0.79	169	6	247	0
Polcevera S12	253	135	2.70	1.54	34	2.21	0.86	391	13	19	0
Polcevera S13	1001	110	2.20	1.25	26	1.89	0.88	191	31	122	0
Polcevera S8	1620	60	1.20	1.60	16	1.13	0.89	103	3	81	0
Slope											
S11	225	150	3.00	1.31	39	2.38	0.87	353	16	100	0
S16	509	43	0.86	2.65	22	1.07	0.91	66	13	56	0
S10	1055	69	1.38	1.52	17	1.64	0.91	88	0	128	0
S7	1516	116	2.32	1.94	15	1.25	0.78	188	6	159	9
S6	2004	128	2.56	1.48	19	1.50	0.72	188	16	194	3

(open slope). At all stations the majority of living foraminifera occurs in the superficial sediment layers. The TSS vertical distribution shows a bimodal curve in the canyon stations while unimodal patterns are observed in the slope stations except for S7, which shows a more irregular curve (Fig. 4). The average living depth (ALD_5) per station is reported in Table 2. Most of the canyon stations are characterized by a relatively shallow ALD_5 from 1.0 to 1.6 cm except for S1 (Bisagno canyon, 200 m wd) where the ALD_5 values are over 2 cm (2.81 cm). In the slope stations, the ALD_5 ranges from 1.3 to 1.9 exception made for S16 where the ALD_5 value is 2.65 cm.

Bisagno canyon – Three stations (S1, S15, S4) located along the thalweg of the canyon at about 200, 500 and 2000 m depth, were analyzed. The ALD_5 shows a decreasing trend from 200 m (ALD_5 = 2.8 cm) to 2000 m depth (ALD_5 = 1.0 cm). The foraminiferal content shows similar composition and frequencies in S1 and S15 stations, while S4 is quite different. *Bolivina* spp., *Bulimina* spp., *Uvigerina* spp. and *Cassidulina carinata* are the most common taxa from 200 (S1) to 500 m depth (S15). Although they are recorded mainly in 0.5–1 cm and 3–5 cm sediment depth, these taxa are present along the whole 0–5 cm interval. *Globobulimina pyrula* and *Chilostomella oolina* occur mainly at 0.5–1.5 cm interval. In S4 (2000 m) samples, Buliminacaea taxa are replaced by agglutinated species like *Ammolagena clavata, Hyperammina* spp., and *Glomospira charoides*, associated to hyaline taxa like *Eponides pusillus* and *Gyroidina laevigata.* In this station, the maximum density of living foraminifera is at the topmost 0.5 cm of the sediment. Among these species, *G. charoides* is present constantly along 0–5 cm interval while *A. clavata* is recorded exclusively in the surface layer.

Polcevera canyon – Similarly to the Bisagno canyon, three stations located along the thalweg of the Polcevera canyon (about 200, 1000 and 1500 m depth) were analyzed. The ALD_5 ranges from 1.5 (S12, 200 m) to 1.6 cm (S8, 1500 m). In the shallowest station at the canyon head (S12, 200 m depth), the foraminiferal content is similar to S1 of Bisagno canyon although some differences can be highlighted. Similarly to the Bisagno canyon, *Bolivina* spp. and *Bulimina* spp. are abundant but in Polcevera canyon, they are associated to *Valvulineria bradyana*. This species replaces *C. carinata* which is conversely recorded in the Bisagno canyon stations. All these specimens are concentrated in 1.0–1.5 cm interval. With increasing depth (S13, 1000 m depth), agglutinated taxa (*G. charoides, Hyperammina* spp.) show significant frequencies associated to *Bolivina* spp., *Bulimina aculeata*, *C. carinata* and *Uvigerina* spp. The highest frequencies are shifted in the top 1 cm of sediment. In the deepest station (S8) the assemblage appears similar to that observed in the Bisagno canyon at the station (S4) located at comparable depth, although in the Polcevera canyon a more heterogeneous foraminiferal assemblage is observed. It is enriched of significant frequencies of *Melonis* spp., *Bulimina striata* and *Uvigerina mediterranea* recorded in the top 2 cm.

Open slope – Five stations (S11, S16, S10, S7, S6) collected in the depth interval from 200 to 2000 m were considered. At 200 m depth (S11), the foraminiferal content is similar to canyon sites at the same depth. *Bolivina* spp., *Bulimina* spp., *C. carinata* and *U. mediterranea* dominate the foraminiferal assemblages. *Glomospira charoides* and *Cibicides pachyderma* are present too. The maximum concentration of specimens is recorded at 0.75 cm and 1.75 cm in the sediment, although these taxa are recorded down to 4 cm. At 500 m depth (S16), the assemblage is more diversified, but it is concentrated between the surface and 2 cm down in the sediment. With increasing depth few dominant species (*G. laevigata* and agglutinated taxa like *G. charoides*, *Hyperammina* spp.) are recorded, showing a more irregular vertical distribution except for the deepest station (S6, 2000 m) which displays a gradual decreasing of foraminiferal content from the surface to 5 cm down in the sediment (unimodal pattern, Fig. 4). The presence of the *Amphistegina* genus, a macroforaminifer typical of warm water, is recorded in the surface samples (0–0.5 cm interval, S16).

4.3.2. Statistical analyses

The dendrogram derived from HCA highlights two main clusters corresponding to distinct assemblages (Fig. 8): assemblage *a*, including stations S1, S15, S12, S11 and S13 and assemblage *b*, that includes S6, S7, S4, S8 and S10 (Table 3). Moreover, the cluster grouping depicts a single outlier station (S16, *c* in Fig. 8a), located in the upper slope west of Polcevera canyon. The spatial distribution of the two main assemblages (Fig. 8b) shows that assemblage *a* gather all stations belonging to the upper sector of the canyon axes, directly located in front of the city of Genoa and its harbor or collected laterally to Polcevera canyon in the adjacent coastal open slope. Conversely, the assemblage *b* groups more offshore stations located either in the middle and lower canyons as well as in the open slope (Fig. 8b).

The characterizing species of assemblage *a*, as determined by SIMPER analysis, mainly includes Bolivinids (*Bolivina* spp. > 20%), Buliminids (*Bulimina* spp. mean value of 17.2), *Uvigerina* spp. (mean value 16.2%) and *C. carinata* (mean value 13.0%). However, some differences are evident between the open slope site (S11) and the canyon sites (S12, S13, S1, S15). In fact, the first shows a lower bolivinids content but the exclusive presence of *Gavelinopsis lobatulus*, *Globocassidulina subglobosa*, *Cassidulina crassa* and more diversified agglutinated taxa (*Bigenerina cylindrica, Labrospira subglobosa, Eggerelloides scabra*) (Appendix A).

Assemblage *b* shows the dominance of *G. charoides* (mean values 35.00%) and *Gyroidina* spp. (mean value 28.25%). *Hyperammina* spp. and *Uvigerina* spp. follow with 15.00% and 18.25% mean values respectively. *Eponides pusillus, Melonis* spp., *A. clavata, Ammodiscus planorbis* and *G. subglobosa* are also present with frequencies ranging from

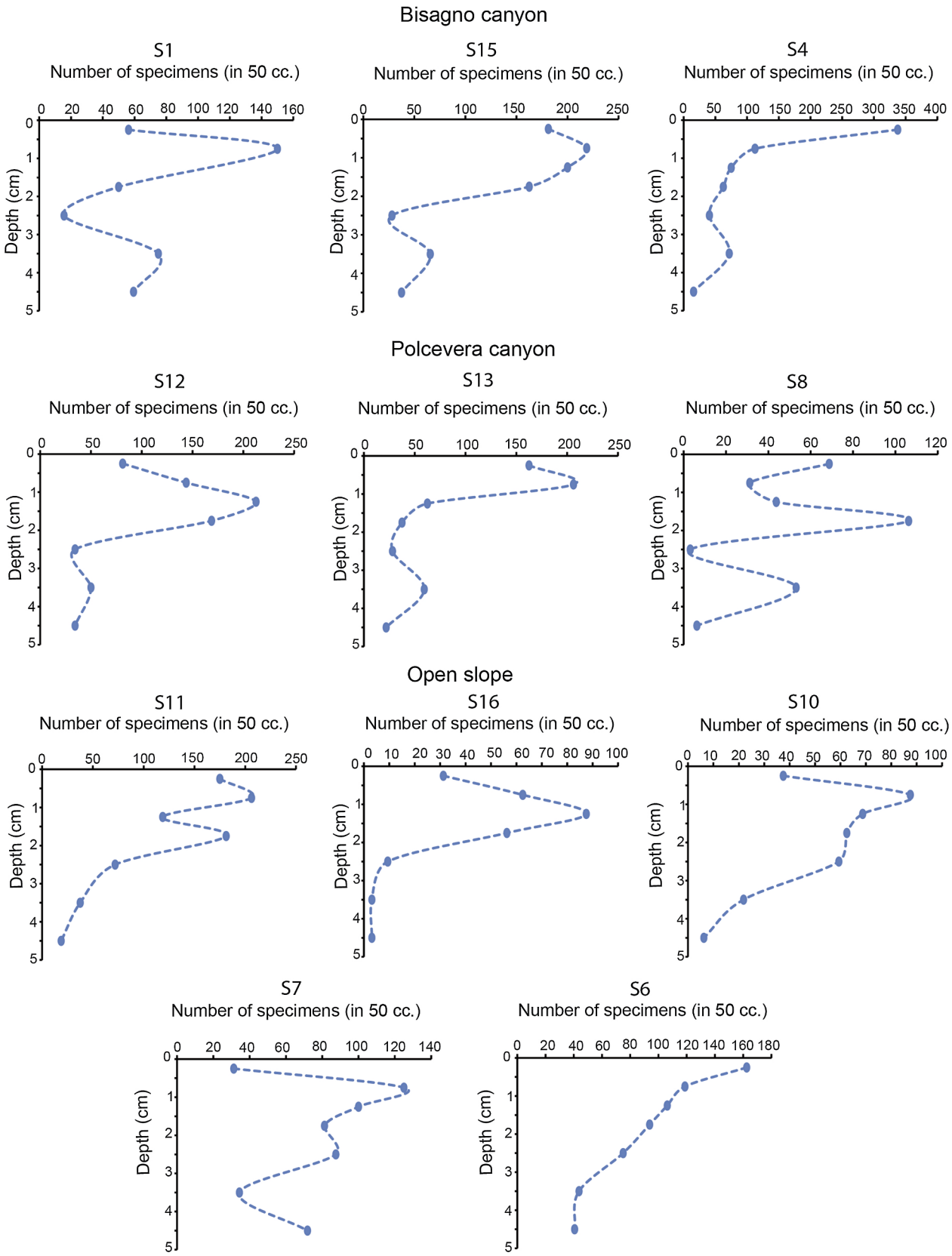


Fig. 4. Vertical distribution of Total Standing Stock (TSS) in the sediment profile at each station.

6.00 to 9.00%. With increasing depth (S7, S6), the dominance of *Gyroidina* genus is associated to high frequencies of agglutinated taxa, with values ranging from 12.50 (*Hyperammina* spp.) to 23.50% (*G. charoides*). *Ammodiscus planorbis* follows with frequencies of 9.50%. *Melonis* spp., *C. carinata* and *Bolivina* spp. are present with frequencies ranging from 1.50% to 4%. Among these groups of taxa are also

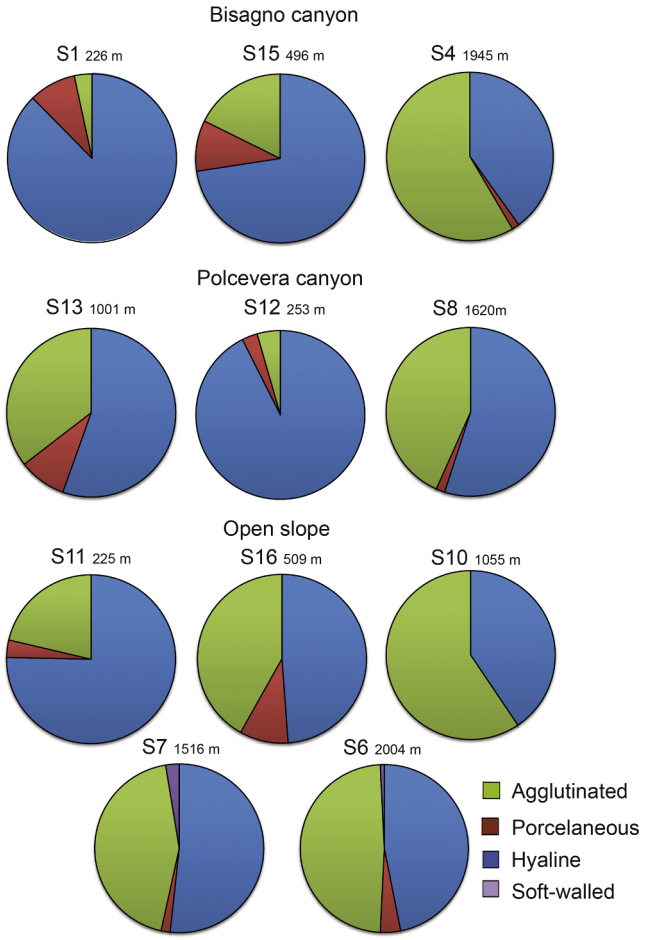


Fig. 5. Test composition of living (stained) foraminifera in the studied area. Each pie chart is based on values from 0 to 5 cm below surface layer (bsl) sediment intervals.

included *Nodellum* sp. and *Hospitella* sp., the only two soft-walled taxa recorded in the study area.

The sample S16 is characterized by frequent *G. charoides* (32.65%), *U. mediterranea* (20.99%), *Amphicoryna scalaris* (16.32%) and *Melonis barleeanus* and *Bigenerina nodosaria* (13.99%). The assemblage includes also a peculiar taxon, *Amphistegina lessonii*, a larger symbiont-bearing foraminifer, abundant in tropical and subtropical reef and shelf regions of the world's oceans (Langer and Mouanga, 2016). The pair-wise comparison of the SIMPER routine shows that the sample S16 differs from the assemblage *a* primarily for the extreme paucity of Bolivinids and Buliminids, whereas the absence of *Gyroidina* spp. and the low abundance of *Hyperammina* spp. determine the largest differences of this sample from the assemblage *b*.

The nMDS plot (Fig. 8c) confirms the results obtained from the HCA by segregating two main groups of stations corresponding to the assemblage *a* and *b*, whereas the station S16 (assemblage *c*) stands alone in the plot (Fig. 8c).

The significance of the differences among the assemblages *a*, *b* and the sample S16 (assemblage *c*) is also confirmed by the results of ANOSIM test (p-value ≤ 0.001, Global R = 0.97).

4.3.3. Canonical correspondence analysis

Canonical Correspondence Analysis (CCA) based on foraminiferal assemblages (abundance of different type of test and species > 10%, 0–5 cm) and environmental data (depth, temperature, salinity and organic matter parameters) is shown in Fig. 9. Two different outputs came from CCA analysis both referred to the most abundant species (Fig. 9) and the groups of different test (agglutinated, porcelaneous or hyaline) (Fig. 10) together with depth, water masses features (temperature, salinity) and organic matter. In both Figs. 10 and 9, CCA the horizontal axes (axis 1) explain 55.59% (eigenvalue = 0.59) and 87.95% (eigenvalue = 0.17) of the total variance in the foraminiferal data, respectively (p-value < 0.001). In Fig. 9A, two opposite groups of variables appear to be most responsible of the separation between coastal and offshore sector stations. The depth reflects the major gradient along which foraminiferal assemblages distribute. Labile and semi-labile components (phytopigments, proteins, lipids) with dissolved oxygen, salinity and temperature are inversely correlated to depth, as opposite to more refractory carbohydrates. Similarly, the species distribution shows two groups associated to the same environmental variables reflecting the clustering dendogram (HCA), displaying the cluster *a* on the right and the cluster *b* on the left side of the diagram (Fig. 9B).

Cluster *c* including only S16 appears slightly different from the other coastal samples because of the higher carbohydrates content (Appendix A). The foraminiferal assemblage *a*, mainly consisting of hyaline taxa, is inversely correlated with depth and carbohydrates and positively with lipids and proteins (Fig. 10) which show their highest values towards the coast (Fig. 9). On the contrary, the assemblage *b*, characterized by high percentages of agglutinated species, is strictly correlated to depth and carbohydrates and inversely correlated to lipids and proteins (Fig. 10). Porcelaneous and soft-walled groups show an opposite distribution although they are plotted at maximum distances from the variables and axes.

Among the species, it is noteworthy to observe that *G. charoides* is associated to carbohydrates, while *B. spathulata* and *Bulimina* spp. to lipids and proteins respectively (Fig. 9B).

5. Discussion

Our results show that foraminiferal assemblages either in canyons and adjacent open slope display abundances and diversity values similar to those of canyons characterized by strong sediment transport (Hess et al., 2005; Koho et al., 2007; Hess and Jorissen, 2009). This is consistent with the fact that sampling period was at the end of the winter season, when the weathering conditions favored the riverine input linked to the torrential regime of the Polcevera and Bisagno rivers (Migeon et al., 2011). TSS decreased along the canyon axes moving from the head to the distal and deeper portions of the canyons, as observed in other submarine canyons of the western Mediterranean Sea (Contreras-Rosales et al., 2012).

However, conversely to previous observations (Koho et al., 2007; Fontanier et al., 2008; Nardelli et al., 2010; Bolliet et al., 2014; Di Bella et al., 2017), foraminiferal assemblages did not show clear differences in species composition between canyons and open slope domains. In the present study, as both HCA and CCA analyses suggest, the distance from the coast (i.e. coastal vs offshore sectors) seems to represent one of the main drivers explaining the distribution of foraminiferal assemblages (Fig. 8b and c). Here, two sectors can be recognized: (1) the coastal range that includes all the stations near the coast located both in open slope (S11) and canyons' head (S1, S12, S13, S15) (assemblage *a*); (2) the offshore sector, characterized by deep stations in the open slope (S6, S7, S10) and along the axes of Polcevera and Bisagno canyons (S4, S8) (assemblage *b*). The station S16 representing the assemblage *c*, located at 500 m, shows intermediate features between the assemblages from both sectors (*a* and *b*); however, when compared to the assemblage *a* (coastal sector), because of the dominance of *G. charoides* and the decrease of Buliminids and Bolivinids, it was included in the offshore sector.

In the following lines we discuss the data considering the different foraminiferal fauna structure in the coastal and offshore sector respectively as modelled by environmental drivers. A particular situation is found at the station S16 where we identified a tropical symbiont bearing species *A. lessonii*. *Amphistegina lessonii* is a tropical species so

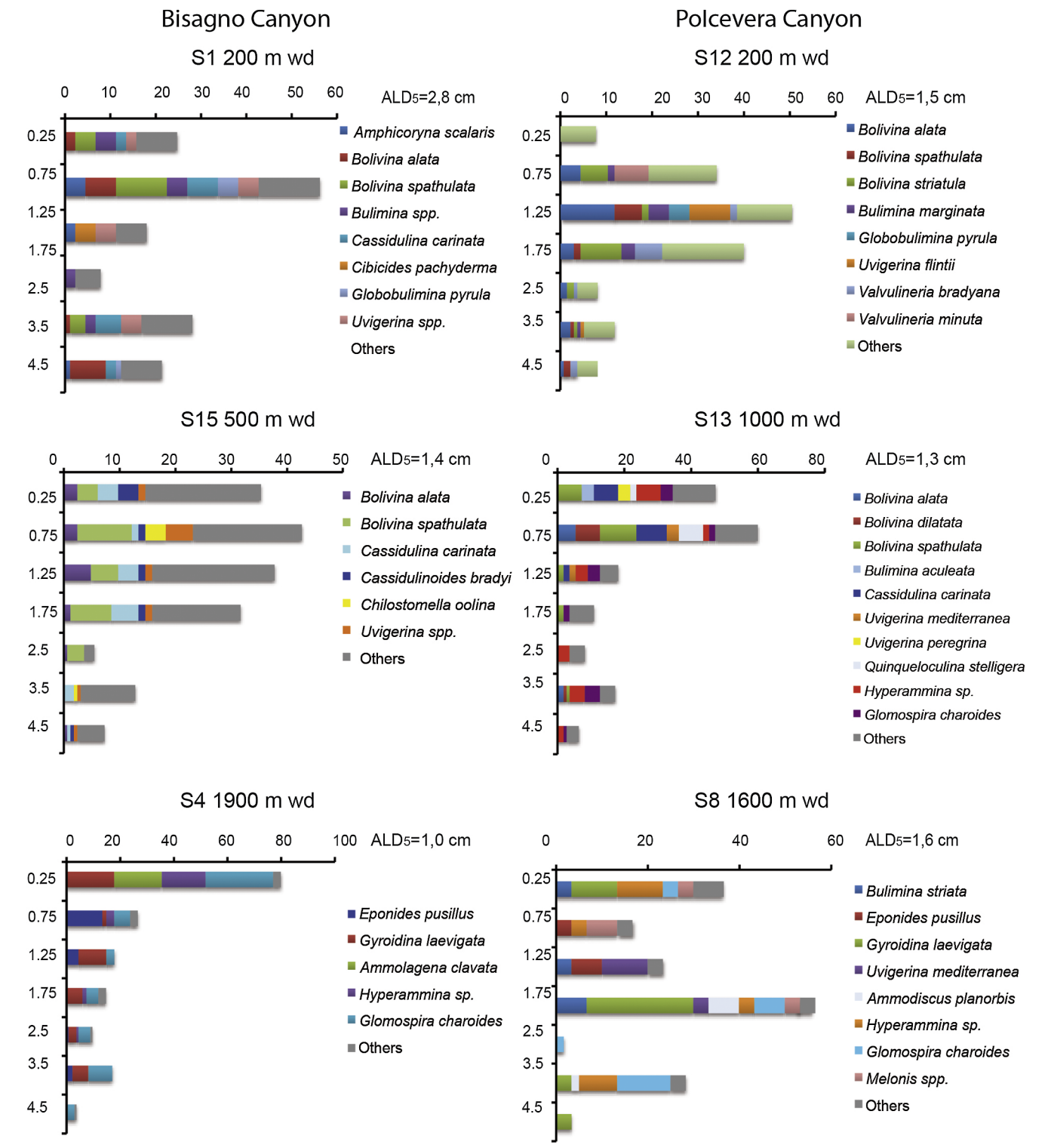


Fig. 6. Vertical distribution of the living (stained) foraminifera in the Bisagno and Polcevera canyons. In the diagrams, only the species making up more than 4% of the total standing stock per station are represented. In the figure, the Average Living Depth (ALD) value is also reported.

far recorded in the south/eastern part of the Mediterranean. This species was encountered in all of the open-slope sites, but was particularly abundant at S16. The identification of the specimens *A. lessonii* at 500-m depth (S16) in the Ligurian Sea is anomalous and relevant. In fact, based on the knowledge of this taxon, it is difficult that this species can live at this depth, being a larger symbiont-bearing foraminifer (Nezlin et al., 2004). For this reason, although these specimens were stained with Rose Bengal, it cannot be excluded that these living specimens were transported at higher depths by bottom currents. Despite this, this finding is highly relevant because allows us to hypothesize a northward migration of this species due to warming climate change affecting the western sector of Mediterranean Sea (Langer and Mouanga, 2016; Danovaro et al., 2017, 2018).

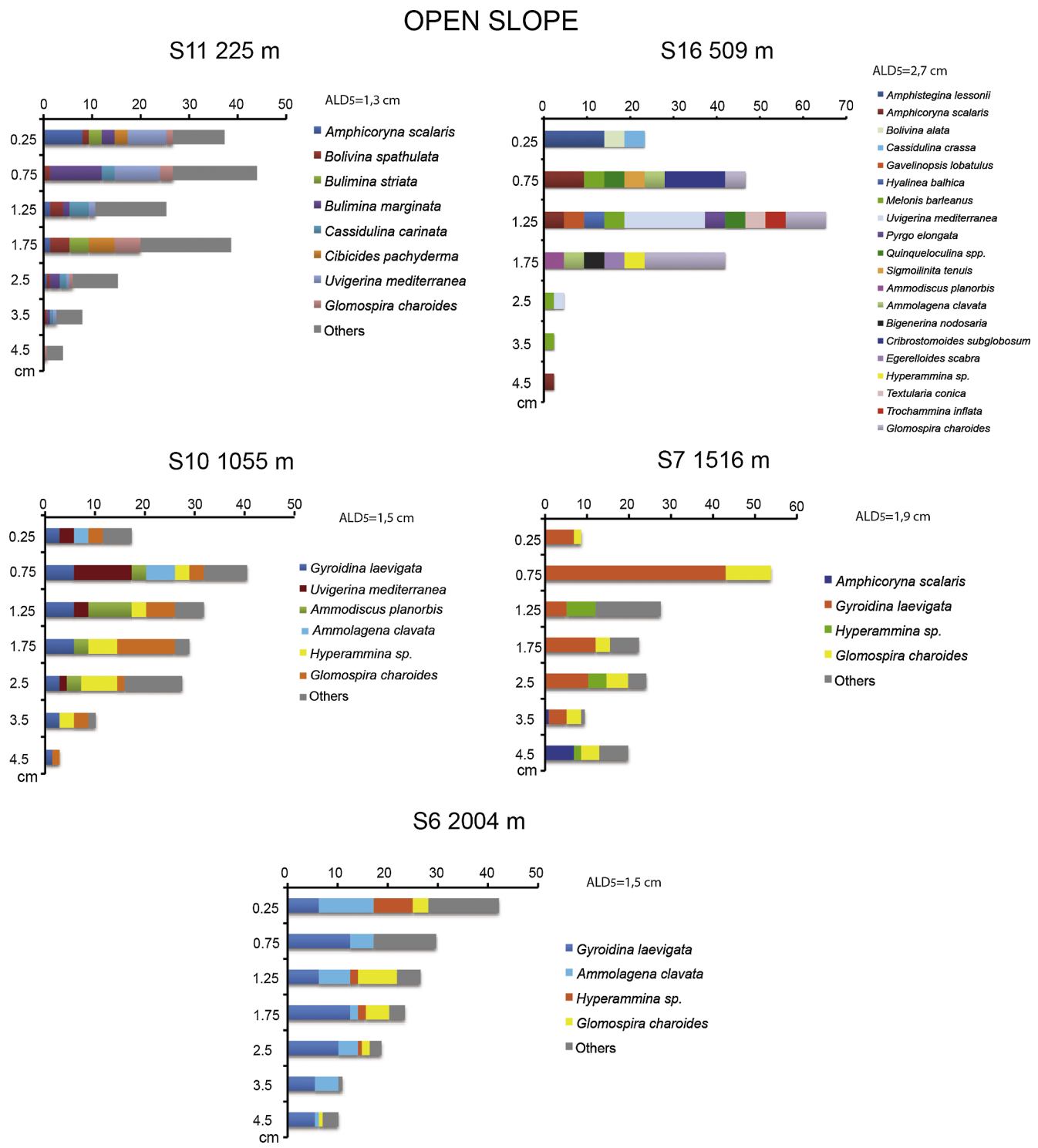


Fig. 7. Vertical distribution of the living (stained) foraminifera in the open slope sectors. In the diagrams only the species making up more than 4% of the total standing stock per station are represented. In the figure the Average Living Depth (ALD) value is also reported.

5.1. Coastal sector

This sector includes mainly canyons' head sites and the shallowest station of the open slope. This area is strictly influenced by river inputs because of its vicinity to the coast, and it is characterized by a foraminiferal assemblage (cluster *a*, Fig. 8b and c) mainly consisting of hyaline infaunal species like Bolivinids, Buliminids, and Uvigerinids. These taxa generally occur in muddy sediments that are characterized by high organic matter content (Jorissen, 1988; Corliss, 1991; Schmiedl et al., 2000; Fontanier et al., 2008). Their maximum concentration in the study area is reported in front of the Bisagno and Polcevera river mouths (Kaiser et al., 2014). Beside the continental input, the organic matter enrichment in this area can be explained by a complex combined action of the coastal upwelling triggered by transient winds and the complex geomorphological setting of the sea-bottom and the coastline (Nezlin et al., 2004). The intensity and entity of these processes is mainly dependent on the meteorological conditions and seasonal variability, however generally, in wintertime they are stronger than in

Table 3
Summary of the foraminiferal assemblages carried out from Q-mode Hierarchical Cluster Analysis. S and H are reported as mean values.

Station	Depth (wd) m	Cluster	Foraminiferal assemblage
Bisagno S1	226	*a*	*a: Bolivina* spp. (31.4%), *Bulimina* spp. (17.2%), *U. peregrina* (16.2%), *C. carinata* (13.0%). S = 36; H = 2.45
Bisagno S15	496	*a*	
Polcevera S12	253	*a*	
Polcevera S13	1001	*a*	
Open slope S11	225	*a*	
Open slope S10	1055	*b*	*b: G. charoides* (35.0%), *Gyroidina* spp. (28.2%), H*yperammina* spp.(18.2%), *Uvigerina* spp. (15%). S = 16; H = 2.18
Polcevera canyon S8	1620	*b*	
Bisagno canyon S4	1945	*b*	
Open slope S7	1516	*b*	
Open slope S6	2004	*b*	
Open slope S16	509	*c*	*c: Gyroidina* spp. (70.0%), *G. charoides* (23.5%), *A. clavata* (19.5%), Hyperammina spp. (12.5%). S = 17; H = 1.80

summer season. In another area of the northwestern Mediterranean Sea (Gulf of Lions), these mechanisms may induce events of dense shelf water cascading, which influence significantly the organic matter inputs and sediment dynamics (Nardelli et al., 2018). However, in the studied canyons, the phenomenon of dense water cascading appears to be absent, as also testified by the overall homogeneity in the hydrological variables observed during the cruise. The biochemical composition of sediment organic matter reported in the present study is consistent with previous literature regarding the trophic conditions in this sector, with very high values of biopolymeric C and total phytopigments (Fig. 3). In particular, the values of biopolymeric C observed in this sector, ranging between 1.8 and 2.7 mgC g^{-1}, suggest conditions close to eutrophication (Pusceddu et al., 2009), which are consistent with the occurrence of abundant infaunal species typical of eutrophic conditions (*Bulimina* spp. and *Bolivina* spp.). Moreover, it is well known that foraminiferal distribution generally depends not only on the quantity but also on the quality of organic matter (e.g. Van der Zwaan, 1982; Gooday, 1988; Altenbach and Sarnthein, 1989; Corliss and Emerson, 1990; Corliss, 1991; Loubere et al., 1993; Rathburn and Corliss, 1994; Fariduddin and Loubere, 1997; Jorissen et al., 1998; De Rijk et al., 2000; Licari et al., 2003; Hess and Jorissen, 2009; Nardelli et al., 2010). The higher accumulation of organic matter and the presence of detritus patches can promote higher abundances and diversity of benthic organisms (Bianchelli et al., 2010; Fernandez-Arcaya et al., 2017). Indeed, here we recorded the highest values of TSS and H at 500 m in the Bisagno canyon where we also found the highest contribution of phytopigments to biopolymeric carbon (50%). Recent studies highlighted that both lipid and protein concentrations in the sediments could significantly influence the foraminiferal distributions (Sabbatini et al., 2012, and references therein). In this study the CCA analysis further supports this hypothesis. Species characterizing assemblage *a* like *Globulimina affinis, B. spathulata, Bulimina alazanensis* and *C. carinata* (Fig. 11) are associated to lipids that are considered a more labile organic compound (Grémare et al., 2002, 2003; Fontanier et al., 2008). According to our CCA analysis, *Bulimina* spp. (*Bulimina aculeata, B. marginata* and *B. striata*) are correlated to proteins, which suggest that they are more sensitive to proteins. In the same assemblage (*a*), epifaunal or shallow infaunal taxa like *U. mediterranea, M. barleeanus*, *G. subglobosa*, and *G. lobatulus*, were also recorded. These species generally live in sediments enriched in labile organic matter or in environments characterized by moderate-high organic-matter fluxes (Fontanier et al., 2008 and reference therein). They are strictly associated to dissolved oxygen content than *Bulimina* spp. suggesting nearly meso-eutrophic conditions. Significant frequencies of miliolid species (porcelaneous group) provide further support to this hypothesis because these taxa typically feed on fresh detritus (e.g., Gooday, 1988). Such trophic conditions are furthermore consistent with the relatively high values of the total phytopigments concentrations (ranging from 10.3 to 24.4 μg g^{-1}) both in canyon and slope sites in this sector of the entire study area. However, a slight difference between the canyon (head) and the open slope sites is evidenced by the different composition of the foraminiferal assemblages. In fact, in the open slope station, the epifaunal species (*C. pachyderma*) increase, together with the relatively high frequency of *G. subglobosa*, a phytodetritus feeder preferring fresh nutrient supply such as diatoms (e.g. Fariduddin and Loubere, 1997; Murray, 2006), and *G. charoides* (Fig. 11) which is common in oligotrophic environments (e.g. De Rijk et al., 2000). This change is associated to a decrease of *Bolivina* spp. frequencies (low oxygen species) and suggests a more oligothrophic setting when compared to the canyon stations, where organic particles are trapped by the canyon geomorphology (Corliss, 1979; Mackensen et al., 1995; Eberwein and Mackensen, 2006). Moreover, at the Polcevera canyon head (S12), the presence of *V. bradyana* is noteworthy and suggests an organic matter enrichment and dysoxic environment (Fontanier et al., 2002; Murray, 2006; Frezza and Carboni, 2009). Although at the Bisagno canyon head we reported the highest biopolymeric C concentrations, we cannot exclude a negative impact on faunal abundance exerted by the heavy industrial activities of the coastal area. Previous studies, indeed, highlighted the impact of anthropic pollution on foraminiferal assemblages resulting in the decrease of the faunal abundance and biodiversity, along with an altered assemblage composition (e.g., Cearreta et al., 2002; Elberling et al., 2003; Hayward et al., 2004; Scott et al., 2005; Romano et al., 2008; Ruiz et al., 2008; Bergamin et al., 2009; Debenay and Fernandez, 2009; Ferraro et al., 2009; Frontalini et al., 2010; Dolven et al., 2013; Benito et al., 2015). A confirmation that frequent derivative oil products largely impact the seafloor between 200 and 2000 m depth is provided by the analysis of the sediment samples here studied, where tests of foraminifera appear to be incorporated in tar (Fig. 3) and given the high heavy metals concentrations recorded by Papale et al., in the same crusise (2018), thus evidencing the strong anthropogenic impact across the area off the Genoa harbor.

At all the coastal stations, the irregular vertical distribution and the mixing of taxa characterized by differently specialized microhabitats in the sediment (epifaunal, shallow and deep infauna), point to physical disturbances occurring in canyon and open slope sites (high sedimentation rates, high slope angle, hyperpycnal flows) and support wide unstable sedimentary conditions (Migeon et al., 2011). It cannot be excluded that many species, commonly occurring in the studied samples, may represent “recolonizers” after environmental disturbance (e.g. *B. spathulata*) (Contreras-Rosales et al., 2012). High hydrodynamic conditions are suggested by significant frequencies of *C. carinata,* typical taxon of high–energy environments and sustained food input (Hayward et al., 2002; Murray, 2006, Duchemin et al., 2008; Mojtahid et al., 2009; Di Bella et al., 2017) and local presence of coarse grainsize sediment (S15). We might suppose that the combined effect of different factors, related to the oceanographic setting and the seasonal food availability linked to periodical sedimentary fluxes, causes widespread mesotrophic seafloor conditions resulting in a homogenization of foraminiferal assemblages in the proximity of the coast (both canyons and open slope). On the other hand, similar foraminiferal distributions are observed in other sectors of western/central Mediterranean basin (e.g.

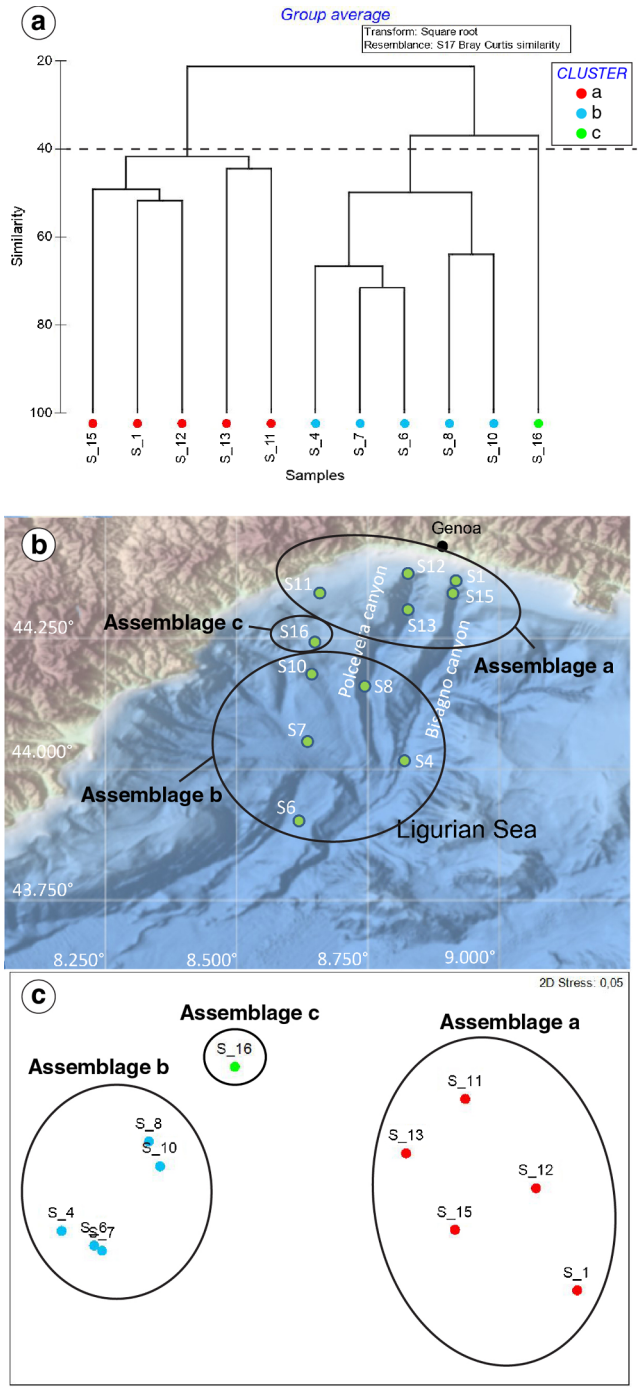


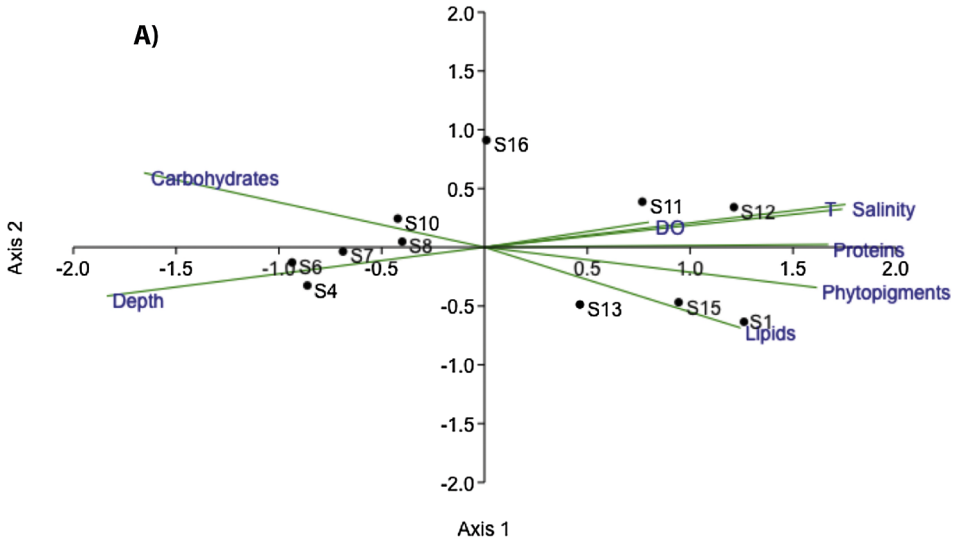
Fig. 8. (a) Dendrogram of the Q-mode hierarchical cluster analysis of species data. The colored dots indicate the identified assemblages and the colors refer to the legend in the upper right inset. (b) Bathymetric map showing the spatial distribution of the assemblages. (c) Two-dimensional ordination plot from non-metric multidimensional scaling of species data. Samples are grouped according to the assemblages resulting from the cluster analysis and the colors of the samples refer to the legend in (a).

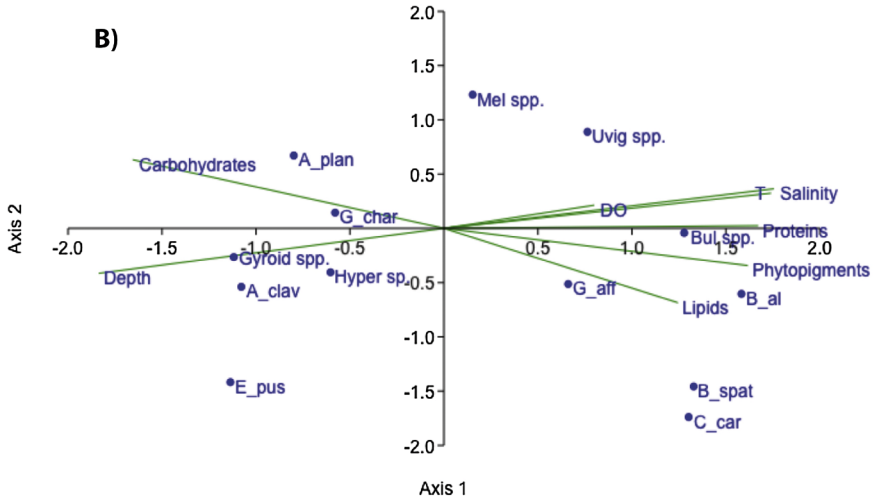
the Calabrian coast of the Tyrrhenian Sea), where similar geo-morphological setting occurs, although in presence of quite different oceanographic conditions (Pierdomenico et al., 2016; Di Bella et al., 2017).

5.2. Offshore sector

The hypothesis that the physical disturbance related to sedimentary flows decreases in the offshore sector in relation to larger distances from the coastline is reasonable. However, although this more stable sedimentary context should favor the benthic life, a decrease in faunal abundance and diversity is here recorded. The decrease of the labile fraction of organic matter was associated to the decrease of faunal abundance with increasing water depth. In the open slope, the low TSS values from 500 (S16) to 1000 m (S10) are associated to a change in the organic matter composition, in terms of the lowest lipid contribution to the biopolymeric pools (ca. 10%) and the highest carbohydrate fraction (59%). This finding support the hypothesis of a significant role played by lipid content for the foraminiferal community (Fontanier et al., 2008; Sabbatini et al., 2012). Overall, the reduction of lipids and proteins with the depth is balanced by the increase of carbohydrate content. This translates into a consistent foraminiferal change consisting in a strong increase of agglutinated taxa. In fact, the assemblages *b* and *c* are mainly characterized by typical deep-sea communities like *G. laevigata, Uvigerina* spp., *E. pusillus*, (Murray 2006; Koho et al., 2007; Nardelli et al., 2010) associated to very abundant *G. charoides* (Fig. 8b and c). The last species occurs mainly in deep-sea environments characterized by natural disturbance processes under oligotrophic conditions (Kaminski et al., 1988; Jonasson et al., 1995; De Rijk et al., 2000; Contreras-Rosales et al., 2012; Di Bella et al., 2016; Nardelli et al., 2018), showing an opportunistic behavior similarly to *B. spathulata* in the shallower sector. However, while *B. spathulata* seems strictly related to high lipids content in the proximal sector, *G. charoides* appears analogously correlated to carbohydrates content and depth. The dominance of *G. charoides,* associated to relatively high abundances of living fauna, mainly consisting of shallow infaunal, and/or epifaunal taxa and the decrease of ALD_5, suggests a stage of re-colonization after a possible mass depositional event. In fact, *Glomospira charoides* was also reported as “disaster species” (e.g., Alegret et al., 2009), an early colonizer after strong disturbance. Similar conditions seem to occur also in the Nazaré canyon, in the Portuguese margin, and in the Cap de Creus canyon in the NW Mediterranean basin (Nardelli et al., 2010, 2018). In the samples collected from the deepest sites (S7, S6) a clear increase of agglutinated shallow infaunal taxa (*A. clavata, G. charoides* and *Hyperammina* spp.) occurs associated to high frequencies of epifaunal species like *G. laevigata*. We suggest that this compositional change relates to the WMDW which affect only these deep stations, as reported by Luna et al. (2013). This current is cooler and more oxygenated than LIW and it could favor the abundance of these taxa often considered to be less tolerant of low oxygen conditions and less dependent on fresh food inputs than calcareous foraminifera feeding instead on more refractory material (e.g. Gooday, 2003; Gooday et al., 2008; Koho et al., 2008; Phipps et al., 2012; Caulle et al., 2014).

Noteworthy, a closely related assemblage is recorded by Contreras-Rosales et al. (2012), in the lower axis of canyon and slope at the Cap de Creus canyon under oligotrophic conditions. This is also supported by the presence, exclusively in these stations, of soft-walled taxa (e.,g. *Nodellum* sp.) typical of bathyal oligotrophic settings. Although the record of soft-walled taxa exclusively from these sites could be also related to the low preservation degree of their tests, this might be read as a further evidence of the major impact of physical disturbance affecting the coastal sectors with respect to the offshore. Similarly to the Cap de Creus canyon area, in our deeper stations (S7 and S6) the minimum phytopigments values of the study area (S7: 3.8 and S6: 2.4 μg/g) are associated to a decrease of organic matter quality (low values of Chl-a, Appendix A). Given the similarity with the Cap de Creus canyon assemblages and the tightly connection of the Ligurian Sea with the Gulf of Lion (Astraldi et al., 1995), we suggest that the deepest portion of the slope could be also influenced, even if only marginally, by the similar hydrodynamic conditions, consisting of the interaction between the open-ocean convection and possible dense shelf water cascading (Nardelli et al., 2018). This complicated hydrodynamic setting could lead to the same oligotrophic conditions (in terms of organic matter concentration) with the consequent development of similar





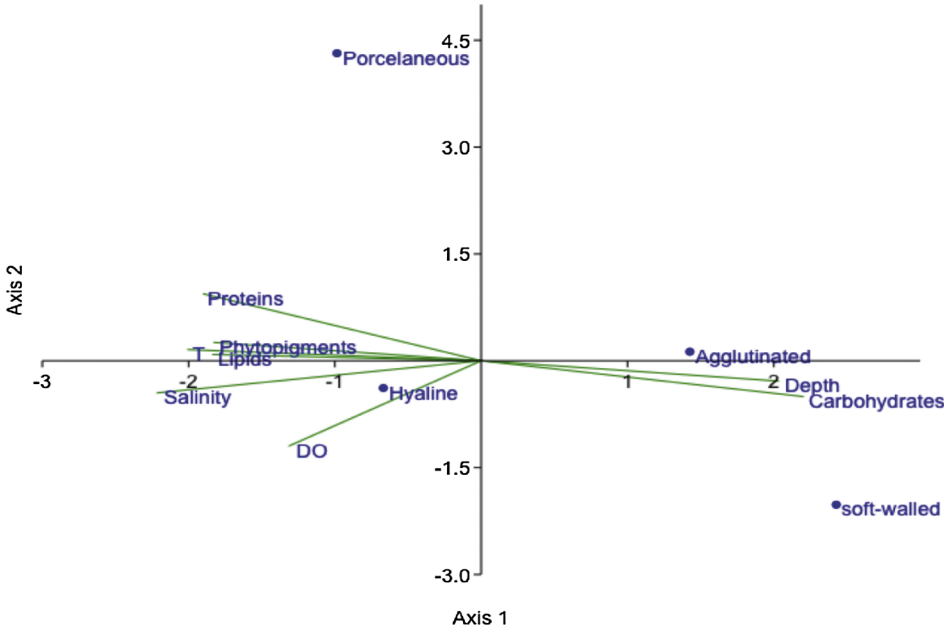


Fig. 9. Canonical Correspondence Analysis (CCA) diagrams of (A) stations-environmental variables (temperature, dissolved oxygen and salinity, depth, proteins, lipids, phytopigments and carbohydrates) and (B) foraminiferal species-environmental variables (temperature, dissolved oxygen and salinity, depth, proteins, lipids and carbohydrates). Horizontal axis: Axis 1; Vertical axis: Axis 2. Species abbreviations: A_clav = *Ammolagena clavata*, E_pus = *Eponides pusillus*; Gyroid spp. = *Gyroidina* spp.; G_char = *Glomospira charoides*; Hypers pp. = *Hyperammina* spp.; G_subgl = *Globocassidulina subglobosa*; Mel spp. = *Melonis* spp.; Uvig spp. = *Uvigerina* spp.; B_stria = *Bolivina striatula*; A_scal = *Amphycorina scalaris*; A_les = *Amphistegina lessonii*; G_lob = *Gavelinopsis lobatulus*; Bul spp. = *Bulimina* spp.; G_aff = *Globobulimina affinis*; B_spat = *Bolivina spathulata*; B_al = *Bulimina alazanensis*; C_car = *Cassidulina carinata*.

Fig. 10. Canonical Corresponde Analysis (CCA) diagrams of (a) foraminiferal test groups-environmental variables (temperature, dissolved oxygen and salinity, depth, proteins, lipids, phytopigments and carbohydrates). Horizontal axis: Axis 1; Vertical axis: Axis 2.

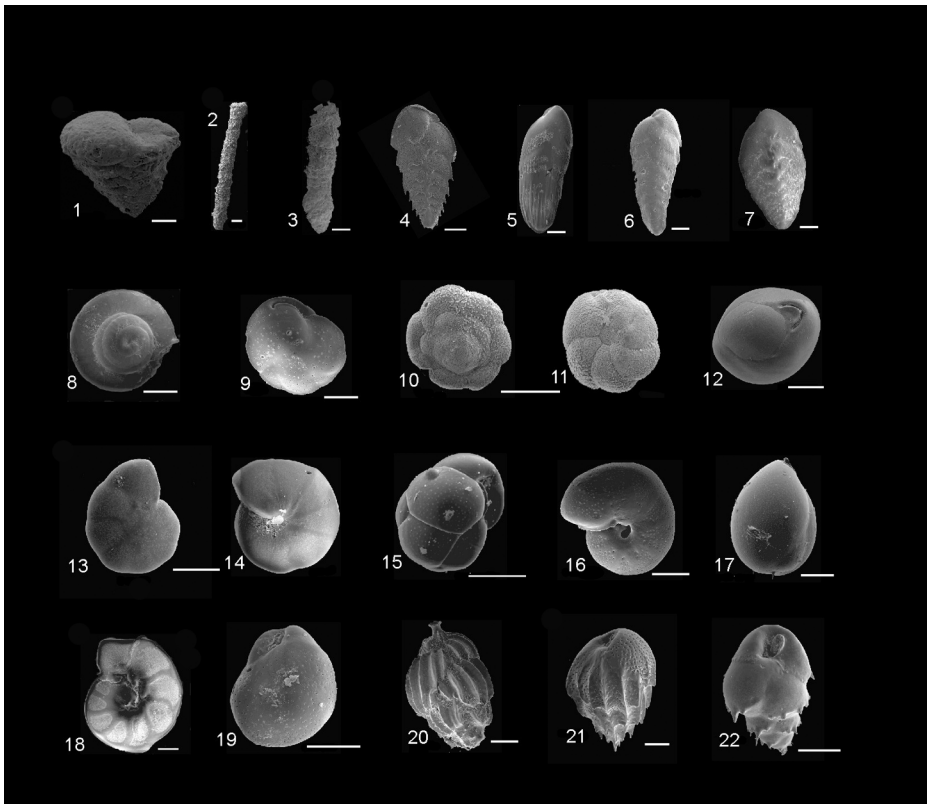


Fig. 11. 1. *Textularia conica* d'Orbigny: side view, S16 – 2. *Hyperammina* sp.: side view, S8 – 3. *Bigenerina nodosaria* d'Orbigny: side view, S10 – 4. *Bolivina alata* (Seguenza); side view, S12 – 5. *Bolivina striatula* Cushman: side view, S12 – 6. *Bolivina spathulata* (Williamson): side view, S15 – 7. *Bolivina dilatata* Reuss: side view, S13 – 8. *Glomospira charoides*: side view – 9. *Cassidulina carinata* Silvestri: apertural view, S13 – 10, 11. *Eponides pusillus* Parr: 10, spiral view; 11, umbilical view, S4 – 12. *Biloculinella globula* (Bornemann): apertural view, S4 – 13, 14. *Gyroidina laevigata* d'Orbigny: 13, spiral view; 14, umbilical view, S8 – 15. *Cassidulina crassa* d'Orbigny: side view, S8 – 16. *Melonis pompilioides* (Fichtel and moll): side view, S15 – 17. *Globulimina pyrula* (d'Orbigny): side view, S12 – 18. *Hyalinea balthica* (Schröter): side view, S6 – 19. *Globocassidulina subglobosa* (Brady): side view, S15 – 20. *Uvigerina mediterranea* Hofker: side view, S. – 21. *Bulimina striata* Guérin and Méneville: side view, S1 – 22. *Bulimina marginata* d'Orbigny: side view, S15. Scale bar = 100 μm.

benthic assemblages and explain the anomalous increase of sandy fraction in this deep sample (S6 4.2%).

6. Conclusions

This study provides new possible insights on the knowledge of the biota and ecosystem functioning of the canyon systems of the Ligurian Sea (NW Mediterranean), which is characterized by a narrow and steep continental margin. Our results suggest that the main factors controlling the distribution and composition of the foraminiferal assemblages are linked more to water depth than to the location in open slope or canyon. Qualitative and multivariate analyses (Hierarchical Cluster Analysis and Canonical Correspondence Analysis) carried out from living (Rose Bengal stained) benthic foraminiferal assemblages allow us to detect two sectors (coastal and offshore) characterized by contrasting trophic features. The coastal sector seems to reflect scattered mesoeutrophic conditions in both physiographic domains, being more impacted by the river inputs and the sediment transport processes. The homogenization of sea-bottom conditions leads to an unclear differentiation between the assemblages inhabiting the open slope and the canyon. The offshore sector appears to be less affected by physical disturbance due to the decrease of the sedimentary flows in relation to larger distances from the coastline. Consequently, the lower organic matter content and lower food quality lead to a more oligotrophic condition, which might favor the development of peculiar assemblages dominated by *G. charoides*, *A. clavata* and epifaunal taxa. Among these taxa, the increase of agglutinated species, mainly *G. charoides*, in the deepest portion of the studied area, could be due to the influence of the WMDW or/and the marginal effects of cascading processes occurring in the nearby sectors of the studied area. Finally, it is worth noting the record of *A. lessonii* at 500-m depth, a tropical species previously reported only in the south/eastern portion of the Mediterranean Sea, which lets us to hypothesize a northward migration of this species associated to the ongoing deep-water warming affecting this highly vulnerable basin.

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Appendix A

Matrix of Cluster Analyses. Quantitative foraminiferal taxa (> 1%).

	S_1	S_15	S_4	S_8	S_12	S_13	S_10	S_7	S_6	S_16	S_11
Alveolophragmium sp.	0	6	0	0	0	0	0	0	0	0	0
Ammodiscus planorbis	0	0	3	16	0	13	38	31	41	6	9
Ammolagena clavata	0	0	75	0	0	0	19	22	131	13	0

Amphicoryna scalaris	16	25	0	0	13	0	0	28	0	22	53
Amphistegina lessonii	0	6	0	0	0	0	0	0	0	19	0
Astacolus crepidulus	16	0	0	0	0	0	0	0	0	0	0
Bigenerina cylindrica	0	0	0	0	6	13	0	0	0	0	13
Bigenerina nodosaria	0	31	0	0	0	0	9	0	0	6	9
Biloculinella depressa	0	0	0	0	9	0	0	0	0	0	0
Biloculinella globula	0	3	13	0	0	13	0	6	19	0	0
Bolivina alata	50	63	0	0	100	25	0	0	0	6	0
Bolivina dilatata	0	3	0	0	13	28	0	0	0	0	13
Bolivina spathulata	53	147	0	0	59	78	6	0	0	0	50
Bolivina striatula	0	6	0	0	78	0	0	0	0	0	0
Bulimina aculeata	13	13	0	0	19	13	0	0	0	0	25
Bulimina striata	0	19	0	25	9	13	3	0	0	0	31
Bulimina elegans	0	0	0	0	0	0	0	0	0	3	0
Bulimina marginata	25	34	0	0	53	6	0	0	0	0	81
Bulimina sp.	6	0	0	0	0	0	0	0	0	0	0
Cassidulina carinata	47	81	0	0	19	6	0	0	0	0	41
Cassidulina crassa	0	0	0	6	0	0	0	0	0	6	19
Cassidulina levigata	0	0	0	0	6	0	0	0	0	0	0
Cassidulinoides bradyi	0	41	0	0	0	0	0	0	0	0	0
Cibicides pachyderma	0	0	0	0	0	0	0	0	0	0	38
Chilostomella oolina	16	22	0	0	28	0	0	0	0	0	0
Cribrostomoides subglobosum	0	0	9	6	19	0	16	9	22	19	3
Dentalina leguminiformis	0	0	0	0	0	0	0	3	6	0	13
Discammina compressa	3	0	0	0	0	3	0	0	0	0	9
Eggerelloides sp.	0	0	0	0	0	0	0	0	0	0	9
Egerelloides scabra	0	9	0	0	0	0	0	0	0	6	22
Elphidium advenum	0	0	0	0	0	63	0	0	0	0	0
Eponides sp.	0	6	88	0	0	0	0	6	9	0	0
Gavelinopsis lobatulus	3	6	6	0	3	0	0	0	0	6	50
Globobulimina ovula	6	0	0	0	6	0	0	0	0	0	0
Globobulimina affinis	0	3	0	6	19	6	0	0	0	0	0
Globobulimina pyrula	16	13	0	0	25	0	0	0	0	0	19
Globocassidulina subglobosa	0	0	0	0	3	0	0	0	3	0	16
Glomospira charoides	0	41	231	44	6	19	63	105	72	44	50
Gyroidina laevigata	0	0	188	75	0	6	59	297	234	0	3
Gyroidinoides umbonata	0	6	0	0	0	34	3	0	0	0	25
Hanzawaia boueana	9	0	0	0	0	0	0	0	0	0	0
Haplophragmoides sp.	0	13	0	0	0	0	0	0	0	0	0
Hoeglundina elegans	0	3	0	0	0	0	0	13	6	0	0
Hospitella sp.	0	0	0	0	0	0	0	0	6	0	0
Hyalinea balthica	13	34	0	0	3	6	0	0	13	6	28
Hyperammina sp.	0	25	91	47	0	3	47	47	47	6	0
Lagenammina atlantica	0	0	0	0	0	0	0	0	0	0	6
Labrospira subglobosa	0	6	0	0	0	0	0	0	0	0	19
Lenticulina sp.	0	0	0	3	0	0	3	0	0	0	0
Lenticulina peregrina	9	0	0	0	0	0	0	0	0	0	6
Lobatula lobatula	0	13	0	0	0	0	0	0	0	0	3
Melonis barleanus	0	13	6	13	25	6	13	6	6	19	6
Melonis pompilioides	3	16	0	13	0	3	0	6	3	0	0
Miliolinella subrotunda	0	6	0	0	0	0	0	0	0	0	0
Neo-lenticulina sp.	0	0	0	0	6	0	0	0	0	0	0
Nodellum sp.	0	0	0	0	0	0	0	16	0	0	0
Nonionella turgida	6	3	0	0	3	0	0	0	0	0	0
Preglobobulimina pupoides	0	0	0	0	6	0	0	0	0	0	0
Pseudotriloculina cf. *rotunda*	0	0	0	0	0	0	0	0	0	0	6
Pyrgo elongata	0	0	0	0	0	0	0	0	0	6	0
Quinqueloculina sp.	0	3	0	0	0	0	0	0	0	0	6
Quinqueloculina padana	0	13	0	0	0	0	0	0	0	6	0
Quinqueloculina pygmaea	0	0	0	0	0	0	0	0	6	0	0
Quinqueloculina seminula	16	16	0	0	0	0	0	0	0	0	0
Quinqueloculina stelligera	0	6	0	0	6	6	0	0	0	6	0
Recurvoides sp.	0	0	0	0	0	0	3	0	0	0	0
Reophax scorpiurus	0	0	0	0	0	0	0	0	0	0	9
Rhabdammina abyssorum	0	6	6	0	0	0	0	0	13	0	0
Rhizammina fragments	0	0	0	0	0	0	6	0	0	0	0
Sigmoilinita tenuis	0	19	0	0	0	31	0	0	0	6	0
Spirillina sp.	0	6	0	0	0	0	0	0	0	0	0
Spiroloculina excavata	6	0	0	0	6	0	0	0	0	0	3
Texularia sp.	0	0	0	0	0	78	0	0	0	0	0
Textularia conica	0	6	0	0	0	0	0	0	0	6	0
Triloculina sp.	9	3	0	0	0	0	0	0	0	0	0
Triloculina cf. *tricarinata*	3	0	0	0	0	13	0	0	3	0	6
Trochammina inflata	0	0	0	3	0	6	0	0	0	6	3
Uvigerina sp.	9	0	0	0	0	0	6	0	0	0	0
Uvigerina flintii	0	13	0	0	41	0	0	0	0	0	0
Uvigerina mediterranea	13	22	0	25	38	19	41	0	0	28	94
Uvigerina peregrina	22	9	0	0	19	19	9	6	0	0	6
Valvulineria bradyana	0	13	0	6	41	0	0	0	0	0	0
Valvulineria minuta	6	0	0	0	31	0	0	0	0	0	0

Matrix of Canonical Correspondence Analysis. Quantitative foraminiferal taxa (> 10%), depth, and organic matter composition ((phytopigments, lipids, proteins and carbohydrates).

Samples	T°C	Salinity	DO (ml/l)	Depth (m)	Phytopigments µg /g	Proteins %	Carbohydrates %	Lipids %	*A_plan*	*A_clav*	*A_scal*	*B_al*	*B_spat*	*B_stria*	*Bul* spp.	*C_car*	*G_subgl*	*E_pus*	*G_lob*	*G_aff*	*Gyroid* spp.	*Hyper* sp.	*Mel* spp.	*G_char*	*Uvig* spp.
S1 0_5	13.5	2.4	4.8	226	10.3	36.3	16.4	36.3	0	0	0	18	19	0	16	17	0	0	0	0	0	0	0	0	16
S15 0_5	13.4	2.1	3.5	496	24.4	43.8	40.0	16.2	0	0	5	12	29	0	13	16	0	0	0	0	0	5	6	8	12
S4 0_5	13.2	1.8	4.1	1946	5.8	30.0	57.3	12.7	0	18	0	0	0	0	0	0	0	21	0	0	44	21	0	55	0
S8 0_5	13.1	1.9	4.1	1624	5.9	33.4	53.5	13.1	8	0	0	0	0	0	13	0	3	10	0	3	40	25	14	23	13
S12 0_5	13.5	2.4	4.7	252	16.0	41.4	40.3	18.3	0	0	3	24	14	19	19	5	4	0	0	4	0	0	6	0	23
S13 0_5	13.3	1.9	3.9	944	10.9	39.0	46.4	14.6	4	0	0	7	23	0	9	18	0	0	0	10	4	23	7	16	9
S10 0_5	13.3	1.9	3.9	1055	5.5	30.8	59.0	10.2	17	9	0	0	3	0	0	0	7	0	0	0	29	22	6	29	26
S7 0_5	13.2	1.9	4.0	1515	3.8	29.5	54.4	16.2	9	6	8	2	4	0	0	4	3	0	0	0	82	13	3	29	0
S6 0_5	13.2	1.8	4.2	2004	2.4	30.8	53.5	15.7	10	33	0	0	0	0	0	0	5	0	0	0	59	12	0	18	0
S16 0_5	13.4	2.1	4.0	507	6.6	38.5	46.1	15.4	5	9	16	5	0	0	0	0	14	0	5	0	0	5	14	33	21
S11 0_5	13.5	2.4	4.6	225	15.1	36.2	44.1	19.7	0	0	11	0	11	0	29	9	0	0	11	0	6	0	0	11	21

Matrix of Canonical Correspondence Analysis. Quantitative foraminiferal groups (> 10%, hyaline, porcelanaceous and agglutinated), depth, and organic matter composition (phytopigments, lipids, proteins and carbohydrates).

Samples	T°C	Salinity	DO (ml/l)	Depth (m)	Phytopigments µg /g	Proteins %	Carbohydrates %	Lipids%	Hyaline	Porcelaneous	Agglutinated	Soft-walled
S1 0_5	13.5	2.4	4.8	226	10.3	36.3	16.4	36.3	244	25	9	0
S15 0_5	13.4	2.1	3.5	496	24.4	43.8	40.0	16.2	372	50	91	0
S4 0_5	13.2	1.8	4.1	1946	5.8	30.0	57.3	12.7	169	6	247	0
S8 0_5	13.1	1.9	4.1	1624	5.9	33.4	53.5	13.1	103	3	81	0
S12 0_5	13.5	2.4	4.7	252	16.0	41.4	40.3	18.3	391	13	19	0
S13 0_5	13.3	1.9	3.9	944	10.9	39.0	46.4	14.6	191	31	122	0
S10 0_5	13.3	1.9	3.9	1055	5.5	30.8	59.0	10.2	88	0	128	0
S7 0_5	13.2	1.9	4.0	1515	3.8	29.5	54.4	16.2	188	6	159	9
S6 0_5	13.2	1.8	4.2	2004	2.4	30.8	53.5	15.7	188	16	194	3
S16 0_5	13.4	2.1	4.0	507	6.6	38.5	46.1	15.4	66	13	56	0
S11 0_5	13.5	2.4	4.6	225	15.1	36.2	44.1	19.7	353	16	100	0

Organic matter biochemical composition. Chlorophyll-a: Chl-a; Chloroplast Pigment Equivalents (phaepigments): CPE; Proteins: PRT; Carbohydrates: CHO; Lipids: LIP; Biopolymeric C: BPC

Samples	Depth (wd) m	Chl-a µg/g	CPE µg/g	PRT mg/g	CHO mg/g	LIP mg/g	BPC mg/g
		m	m	m	m	m	m
Canyon							
Bisagno S1 0_1	226	0.2	10.3	2.6	2.4	0.6	2.7
Bisagno S15 0_1	496	0.5	24.4	1.9	2.2	0.5	2.1
Bisagno S4 0_1	1945	0.1	5.8	0.7	1.7	0.2	1.2
Polcevera S12 0_1	253	0.6	16.0	2.1	2.6	0.6	2.5
Polcevera S13 0_1	1001	0.3	10.9	1.1	1.6	0.3	1.4
Polcevera S8 0_1	1620	0.1	5.9	1.0	1.9	0.3	1.4
Slope							
S11 0_1	225	0.6	15.1	1.3	1.9	0.5	1.8
S16 0_1	509	0.2	6.6	1.0	1.4	0.3	1.2
S10 0_1	1055	0.1	5.5	0.7	2.5	0.2	1.7
S7 0_1	1516	0.1	3.8	0.9	2.0	0.3	1.5
S6 0_1	2004	0.1	2.4	0.8	2.2	0.3	1.3

References

Alegret, L., Ortiz, S., Molina, E., 2009. Extinction and recovery of benthic foraminifera across the Paleocene-Eocene Thermal Maximum at the Alamedilla section (Southern Spain). Palaeog., Palaeocl Palaeoecol. 279, 186–200.

Altenbach, A.V., Sarhein, M., 1989. Productivity record in benthic foraminifers. In: Berger, W.H., Smetacek, V.S., Wefer, G. (Eds.), Productivity of the Oceans: Present and Past. Springer-Verlag, New York, pp. 255–269.

Alve, E., 1995. Benthic foraminiferal responses to estuarine pollution: a review. J. Foraminifer. Res. 25 (3), 190–203. https://doi.org/10.2113/gsjfr.25.3.190.

Astraldi, M., Bianchi, C.N., Gasparini, G.P., Morri, C., 1995. Climatic fluctuations, current variability and marine species distribution: a case study in the Ligurian Sea (northwest Mediterranean). Oceanol. Acta 18, 139–149.

Benito, X., Trobajo, R., Ibáñez, C., Cearreta, A., Brunet, M., 2015. Benthic foraminifera as indicators of habitat change in anthropogenically impacted coastal wetlands of the Ebro Delta (NE Iberian Peninsula). Mar. Poll. Bull. 101, 163–173.

Bergamin, L., Romano, E., Finoia, M.G., Venti, F., Bianchi, J., Colasanti, A., 2009. Benthic foraminifera from the coastal zone of Baia (Naples, Italy): assemblage distribution and modification as tools for environmental characterization. Mar. Poll. Bull. 59, 234–244.

Bianchelli, S., Gambi, C., Zeppilli, D., Danovaro, R., 2010. Metazoan meiofauna in deep-sea canyons and adjacent open slopes: a largescale comparison with focus on the rare taxa. Deep-Sea Res. I 57, 420–433.

Bolliet, T., Jorissen, F.J., Schmidt, S., Howa, H., 2014. Benthic foraminifera from Capbreton Canyon revisited; faunal evolution after repetitive sediment disturbance. Deep-Sea Res. II 104, 319–334.

Bosc, E., Bricaud, A., Antoine, D., 2004. Seasonal and interannual variability in algal biomass and primary production in the Mediterranean Sea, as derived from 4 years of SeaWiFS observations. Global Biogeochem. Cycles 18, GB1005.

Canals, M., Puig, P., de Madron, X.D., Heussner, S., Palanques, A., Fabres, J., 2006. Flushing submarine canyons. Nature 444 (7117), 354–357.

Canals, M., Danovaro, R., Heussner, S., Lykousis, V., Puig, P., Trincardi, F., Calafat, A.M., Durrie de Madron, X., Palanques, A., Sanchez-Vidal, A., 2009. Cascades in Mediterranean submarine grand canyons. Oceanography 22 (1), 26–43.

Casella, E., Molcard, A., Provenzale, A., 2011. Mesoscale vortices in the ligurian sea and their effect on coastal upwelling processes. J. Mar. Syst. 88, 12–19.

Caulle, C., Koho, K.A., Mojtahid, M., Reichart, G.J., Jorissen, F.J., 2014. Live (Rose Bengal stained) foraminiferal faunas from the northern Arabian Sea: faunal succession within and below the OMZ. Biogeosciences 11, 1155–1175.

Cearreta, A., Irabien, M.J., Leorri, E., Yusta, I., Quintanilla, A., Zabaleta, A., 2002. Environmental transformation of the Bilbao estuary, N. Spain: microfaunal and geochemical proxies in the recent sedimentary record. Mar. Poll. Bull. 44, 487–503.

Celussi, M., Quero, G.M., Zoccarato, L., Franzo, A., Corinaldesi, C., Rastelli, E., Lo, Martire M., Galand, P.E., Ghiglione, J.-F., Chiggiato, J., Colucelli, A., Russo, A., Pallavicini, A., Fonda Umani, S., Del Negro, P., Luna, G.M., 2018. Planktonic prokaryote and protist communities in a submarine canyon system in the Ligurian Sea (NW Mediterranean). Progr. Ocean. 168, 210–221.

Chaumillon, E., Deverchére, J., Réhault, J.-P., Gueguen, E., 1994. Réactivation tectonique et flexure de la marge continentale Ligure (Méditerranée Occidentale). Comptes Rendus de l'Académie des Sciences Paris 319, 675–682.

Cimerman, F., Langer, M., 1991. Mediterranean foraminifera. In: Slovenska Akademija Znanosti Umetnosti, Academia Scientiarum Artium Slovenica, Classis IV: Historia Naturalis 30, 1-118.

Clarke, K., Gorley, R., 2006. PRIMER v6: User manual/tutorial. Primer-E Ltd., Plymouth.

Contreras-Rosales, L.A., Koho, K.A., Duijnstee, I.A.P., De Stigter, H.C., García, R., Koning, E., Epping, E., 2012. Living deep-sea benthic foraminifera from the Cap de Creus Canyon (western Mediterranean): faunal-geochemical interactions. Deep-sea Research I 64, 22–42.

Corliss, B.H., 1979. Taxonomy of Recent deep-sea benthonic foraminifera from the southeast Indian Ocean. Micropaleontology 25, 1–19.

Corliss, B.H., 1991. Morphology and microhabitat preferences of benthic foraminifera from the northwest Atlantic Ocean. Mar. Micropaleontol. 17 (3–4), 195–236.

Corliss, B.H., Emerson, S., 1990. Distribution of Rose Bengal stained deep-sea ben-thic foraminifera from the Nova Scotian continental margin and Gulf of Maine. Deep-Sea Res. Part I 37 (3), 381–400.

Covazzi, A., Danovaro, R., Misic, C., 2019. Macrofaunal assemblages in canyon and adjacent slope of the NW and Central Mediterranean systems. Progr. Ocean. 171, 38–48.

Dagg, M.J., Breed, G.A., 2003. Biological effects of Mississippi River nitrogen on the northern gulf of Mexico: a review and synthesis. Jour. Mar. Syst 43, 133–152.

Danovaro, R., 2009. Bioavailable carbohydrates, lipids, and proteins in sediment core 54301–002. PANGAEA. https://doi.org/10.1594/PANGAEA.717341.

Danovaro, R., 2010. Methods for the Study of Deep-Sea Sediments, Their Functioning and Biodiversity. CRC Press, Boca Raton, pp. 428.

Danovaro, R., Corinaldesi, C., Dell'Anno, A., Snelgrove, P.V.R., 2017. The deep-sea under global change. Current Biol. 27 (11), R461–R465.

Danovaro, R., 2018. Climate change impacts on the biota and on vulnerable habitats of the deep Mediterranean Sea. Rendiconti Lincei. Scienze Fisiche e Naturali 1–17.

Debenay, J.P., Fernandez, J.M., 2009. Benthic foraminifera records of complex anthropogenic environmental changes combined with geochemical data in a tropical bay of New Caledonia (SW Pacific). Mar. Poll. Bull. 59, 311–322.

De Rijk, S., Jorissen, F.J., Rohling, E.J., Troelstra, S.R., 2000. Organic flux control on bathymetric zonation of Mediterranean benthic foraminifera. Mar. Micropaleontol. 40 (3), 151–166.

Di Bella, L., Ingrassia, M., Frezza, V., Chiocci, F.L., 2016. The response of benthic meiofauna to hydrothermal emissions in the Pontine Archipelago, Tyrrhenian Sea (central Mediterranean Basin). J. Mar. Syst. 164, 53–66.

Di Bella, L., Pierdomenico, M., Porretta, R., Chiocci, F.L., 2017. Living and dead foraminiferal assemblages from an active submarine canyon and surrounding sectors: the Gioia Canyon system (Tyrrhenian Sea, Southern Italy). Deep Sea Res. I 123, 129–146.

D'Ortenzio, F., Ribera d'Alcalà, M., 2009. On the trophic regimes of the Mediterranean Sea: a satellite analysis. Biogeosciences 6, 139–148.

Dolven, J.K., Alve, E., Rygg, B., Magnusson, J., 2013. Defining past ecological status and in situ reference conditions using benthic foraminifera: a case study from the Oslofjord, Norway. Ecological Indicators 29, 219–233.

Duchemin, G., Jorissen, F.J., Le Loc'h, F., Andrieux-Loyer, F., Hily, C., 2008. Seasonal variability of living benthic foraminifera from the outer continental shelf of the Bay of Biscay. J. Sea Res. 59 (4), 297–319.

Duros, P., Fontanier, C., Metzger, E., Pusceddu, A., Cesbron, F., De Stigter, H.C., Bianchelli, S., Danovaro, R., Jorissen, F.J., 2011. Live (stained) benthic foraminifera in the Whittard Canyon, Celtic margin (NE Atlantic). Deep Sea Res. Part I: Oceanogr. Res. Papers 58 (2), 128–146.

Duros, P., Jorissen, F.J., Cesbron, F., Zaragosi, S., Schmidt, S., Metzger, E., Fontanier, C., 2014. Study of benthic foraminiferal thanatocoenoses from the Cap-Ferret Canyon area (NE Atlantic): a complex interplay between hydro-sedimentary and biological processes. Deep Sea Res. II 104, 145–163.

Eberwein, A., Mackensen, A., 2006. Regional primary productivity differences off Marocco (NW Africa) recorded by modern benthic foraminifera and their stable carbon isotopic composition. Deep Sea Res. II 104, 145–163.

Elberling, B., Knudsen, K.L., Kristensen, P.H., Asmund, G., 2003. Applying foraminiferal stratigraphy as a biomarker for heavy metal contamination and mining impact in a fiord in West Greenland. Mar. Environ. Res. 55, 235–256.

Fabiano, M., Danovaro, R., Fraschetti, S., 1995. A three-year time series of elemental and biochemical composition of organic matter in subtidal sandy sediments of the Ligurian Sea (Northwestern Mediterranean). Cont. Shelf Res. 15, 1453–1469.

Fariduddin, M., Loubere, P., 1997. The surface ocean productivity response to deeper water benthic foraminifera in the Atlantic. Mar. Micropaleontol. 32, 289–310.

Fernandez-Arcaya, U., Ramirez-Llodra, E., Aguzzi, J., Allcock, A.L., Davies, J.S., Dissanayake, A., Harris, P., Howell, K., Huvenne, V.A.I., Macmillan-Lawler, M., Martín, J., Menot, L., Nizinski, M., Puig, P., Rowden, A.A., Sanchez, F., Van den Beld, I.M.J., 2017. Ecological role of submarine canyons and need for canyon conservation: a review. Frontiers in Marine Science 4, 5. https://doi.org/10.3389/fmars.2017.00005.

Ferraro, L., Sammartino, S., Feo, M.L., Rumolo, P., Salvagio, Manta D., Marsella, E., Sprovieri, M., 2009. Utility of benthic foraminifera for biomonitoring of contamination in marine sediments: a case study from the Naples harbour (Southern Italy). J. Environ. Monitor. 11, 1226–1235.

Fishbein, E., Patterson, T., 1993. Error-weighted maximum likelihood (EWML): a new statistically based method to cluster quantitative micropaleontological data. J. Paleontol. 67, 475–486.

Fontanier, C., Jorissen, F.J., Licari, L., Alexadre, A., Anschutz, P., Carbonel, P., 2002. Live benthic foraminiferal faunas from the Bay of Biscay: faunal density, composition, and microhabitats. Deep Sea Res. I 49, 751–785.

Fontanier, C., Jorissen, F.J., Chaillou, G., Anschutz, P., Grémare, A., Griveaud, C., 2005. Live foraminiferal faunas from a 2800 m deep lower canyon station from the Bay of Biscay: Faunal response to focusing of refractory organic matter. Deep Sea Res. I 52, 1189–1227.

Fontanier, C., Jorissen, F.J., Lansard, B., Mouret, A., Buscail, R., Schmidt, S., Kerhervé, P., Buron, F., Zaragosi, S., Hunault, G., Ernoult, E., Artero, C., Anschutz, P., Rabouille, C., 2008. Live foraminifera from the open slope between Grand Rhône and Petit Rhône Canyons (Gulf of Lions, NW Mediterranean). Deep Sea Res. I 55, 1532–1553.

Fontanier, C., Koho, K.A., Goni-Urriza, M.S., Deflandre, B., Galaup, S., Ivanovsky, A., Gayet, N., Dennielou, B., Grémare, A., Bichon, S., Gassie, C., Anschutz, P., Duran, R., Reichart, G.J., 2014. Benthic foraminifera from the deep-water Niger delta (Gulf of Guinea): Assessing present-day and past activity of hydrate pockmarks. Deep-Sea Res. I 94, 87–106.

Frezza, V., Carboni, M.G., 2009. Distribution of recent foraminiferal assemblages near the Ombrone River mouth (Northern Tyrrhenian Sea, Italy). Rev. Micropaleontol. 52, 43–66.

Frontalini, F., Coccioni, R., Bucci, C., 2010. Benthic foraminiferal assemblages and trace element contents from the lagoons of Orbetello and Lesina. Environ. Monitor. Assess. 170, 245–260.

Gerchakov, S.M., Hachter, P.G., 1972. Improved technique for analysis of carbohydrates in sediment. Limnol. Oceanogr. 17, 938–943.

Goineau, A., Fontanier, C., Jorissen, F.J., Lansard, B., Buscail, R., Mouret, A., Kerhervé, P., Zaragosi, S., Ernoult, E., Artéro, C., Anschutz, P., Metzger, E., Rabouille, C., 2011. Live (stained) benthic foraminifera from the Rhône prodelta (Gulf of Lion, NW Mediterranean): environmental controls on a river-dominated shelf. Jour. Sea Res. 65, 58–75.

Gooday, A.J., 1988. A response by benthic foraminifera to the deposition of phytodetritus in the deep sea. Nature 332, 70–73.

Gooday, A.J., 2003. Benthic foraminifera (Protista) as tools in deep-water palaeoceanography: a review of environmental influences on faunal characteristic. Adv. Mar. Biol. 46, 1–90.

Gooday, A.J., Nomaki, H., Kitazato, H., 2008. Modern deep-sea benthic foraminifera: a brief review of their morphology-based biodiversity and trophic diversity. Geolog. Soc., London, Special Publicat. 303, 97–119.

Grémare, A., Medernach, L., de Bovée, F., Amouroux, J.-M., Vétion, G., Albert, P., 2002. Relationships between sedimentary organics and benthic meiofauna on the continental shelf and the upper slope of the Gulf of Lions (NW Mediterranean). Mar. Ecol. Progr. Series 234, 85–94.

Grémare, A., Medernach, L., de Bovée, F., Amouroux, J.M., Charles, F., Dinet, A., Vétion, G., Albert, P., Colomines, J.C., 2003. Relationship between sedimentary organic matter and benthic fauna within the Gulf of Lion: synthesis on the identification of new biochemical descriptors of sedimentary organic nutritional value. Oceanol. Acta 26, 391–406.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistic software package for education and data analysis. Palaeontol. Electron. 4 (1) 9 (178 kb). http://palaeo-electronica.org/2001 1/past/issue1 01.htm.

Harris, P.T., Whiteway, T., 2011. Global distribution of large submarine canyons: geomorphic differences between active and passive continental margins. Marine Geol. 285 (1–4), 69–86.

Hartree, E.F., 1972. Determination of proteins: a modification of the Lowry method that gives a linear photometric response. Anal. Biochem. 48, 422–427.

Hayward, B.W., Neil, H.I., Carter, R., Grenfell, H.R., Hayward, J.J., 2002. Factors influencing the distribution patterns of Recent deep-sea benthic foraminifera, east of New Zealand, southwest Pacific Ocean. Mar. Micropaleontol. 46, 139–176.

Hayward, B.W., Grenfell, H.R., Nicholson, K., Parker, R., Wilmhurst, J., Horrocks, M., Swales, A., Sabaa, A.T., 2004. Foraminiferal record of human impact on intertidal estuarine environments in New Zealand's largest city. Mar. Micropaleontol. 53, 37–66.

Heinz, P., Hemleben, C., 2003. Regional and seasonal variations of recent benthic deep-sea foraminifera in the Arabian Sea. Deep-Sea Res. I 50 (3), 435–447.

Hess, S., Jorissen, F.J., Venet, V., Abu-Zied, R., 2005. Benthic foraminiferal recovery after recent turbidite deposition in Cap Breton Canyon, Bay of Biscay. J. Foramin. Res. 35 (2), 114–129.

Hess, S., Jorissen, F.J., 2009. Distribution patterns of living benthic foraminifera from Cap Breton canyon, Bay of Biscay: faunal response to sediment instability. Deep Sea Res. I 56, 1555–1578.

Jonasson, K.E., Schrijder-Adams, C.J., Patterson, R.T., 1995. Benthic foraminiferal distribution at Middle Valley, Juan de Fuca Ridge, a northeast Pacific hydrothermal venting site. Mar. Micropaleontol. 25, 151–167.

Jorissen, F.J., 1988. Benthic foraminifera from the Adriatic Sea; principles of phenotypic variations. Utrecht Micropaleontol. Bull. 37, 1–176.

Jorissen, F.J., De Stigter, H.C., Widmark, J.G.V., 1995. A conceptual model explaining benthic foraminiferal microhabitats. Mar. Micropaleontol. 26, 3–15. https://doi.org/10.1016/0377-8398(95)00047-X.

Jorissen, F.J., Wittling, I., Peypouquet, J.P., Rabouille, C., Relexans, J.C., 1998. Live benthic foraminiferal faunas off Cap Blanc, NW Africa: community structure and microhabitats. Deep Sea Res. I 45, 2157–2188.

Kaiser, J., Ruggieri, N., Hefter, J., Siegel, H., Mollenhauer, G., Arz, H.W., Lamy, F., 2014. Lipid biomarkers in surface sediments from the Gulf of Genoa, Ligurian sea (NW Mediterranean sea) and their potential for the reconstruction of palaeo-environments. Deep Sea Res. I 89, 68–83.

Kaminski, M.A., Grassle, J.F., Whitlatch, R.B., 1988. Life history and recolonization among agglutinated foraminifera in the Panama Basin. Abh. Geol. Bundesanst. 41, 229–243.

Kitazato, H., Shirayama, Y., Nakatsuka, T., Fujiwara, S., Shimanaga, M., Kato, Y., Okada, Y., Kanda, J., Yamaoka, A., Masuzawa, T., Suzuki, K., 2000. Seasonal phytodetritus deposition and responses of bathyal benthic foraminiferal populations in Sagami Bay, Japan: preliminary results from "Project Sagami 1996–1999". Mar. Micropaleontol. 40 (3), 135–149.

Koho, K.A., Kouwenhoven, T.J., de Stigter, H.C., van der Zwaan, G.J., 2007. Benthic foraminifera in the Nazaré Canyon, Portuguese continental margin: sedimentary environments and disturbance. Mar. Micropaleontol. 66, 27–51.

Koho, K.A., García, R., de Stigter, H.C., Epping, E., Koning, E., Kouwenhoven, T.J., van der Zwaan, G.J., 2008. Sedimentary labile organic carbon and pore water redox control on species distribution of benthic foraminifera: a case study from Lisbon-Setùbal Canyon (southernPortugal). Prog. Oceanogr. 79, 55–82.

Langer, M.R., Mouanga, G.H., 2016. Invasion of amphisteginid foraminifera in the Adriatic Sea. Biol. Invasions. https://doi.org/10.1007/s10530-016-1070-0.

Larroque, C., Béthoux, N., Calais, C., Courboulex, F., Deschamps, A., Déverchére, J., Stéphan, J.-F., Ritz, J.-F., Gilli, E., 2001. Active and recent deformation at the Southern Alps-Ligurian basin junction. Netherland J. GeoSci. 80, 255–272.

Lazzara, L., Marchese, C., Massi, L., Nuccio, C., Maselli, F., Santini, C., Pieri, M., Sorani, V., 2010. Sub-regional patterns of primary production annual cycle in the Ligurian and North Tyrrhenian Seas, from satellite data. Ital. J. Remote Sens. 42, 87–102.

Licari, L.N., Schumacher, S., Wenzhöfer, F., Zabel, M., Mackensen, A., 2003. Communities and microhabitats of living benthic foraminifera from the tropicaleast Atlantic: impact of different productivity regimes. J. Foraminiferal Res. 33, 10–31.

Loeblich, A.R., Tappan, H., 1987. Foraminiferal Genera and their Classification. Van Nostrand Reinhold Comp 970, 44.

Lohrenz, S.E., Dagg, M.J., Whitledge, T.E., 1990. Enhanced primary production at the plume/oceanic interface of the Mississippi River. Cont. Shelf Res. 7, 639–664.

Lohrenz, S.E., Fahnenstie, G.L., Redalje, D.G., Lang, G.A., Chen, X., Dagg, M.J., 1997. Variations in primary production of northern Gulf of Mexico continental shelf waters linked to nutrient inputs from the Mississippi River. Mar. Ecol. Prog. Ser. 155, 45–54.

Lorenzen, C., Jeffrey, J., 1980. Determination of chlorophyll in seawater. Tech. Pap. Mar. Sci. (UNESCO) 35, 1–20.

Loubere, P., Gary, A., Lagoe, M., 1993. Generation of the benthic foraminiferal assemblage: theory and preliminary data. Mar. Micropaleontol. 20, 165–182.

Luna, G.M., and shipboard scientific party, 2013. BioLig - Biodiversity, ecosystem functioning and pelagic-benthic coupling in Ligurian submarine canyons. Cruise Report, 1–78.

Lutze, G.F., Altenbach, A., 1991. Technik und Signifikanz der Lebendfärbung benthischer Foraminiferen mit Begalrot. Geologisches Jahrbuch 128, 251–265.

Mackensen, A., Schmiedl, G., Harloff, J., Giese, M., 1995. Deep sea foraminifera in the South Atlantic Ocean: ecology and assemblage generation. Micropalentology 41 (4), 342–358.

Migeon, S., Cattaneo, A., Hassoun, V., Larroque, C., Corradi, N., Fanucci, F., Dano, A., Mercier de Lepinay, B., Sage, F., Gorini, C., 2011. Morphology, distribution and origin of recent submarine landslides of the Ligurian Margin (North-western Mediterranean): some insights into geohazard assessment. Mar. Geophys. Res. 32, 225–243.

Milker, Y., Schmiedl, G., 2012. A taxonomic guide to modern benthic shelf foraminifera of the western Mediterranean Sea. Palaeontologia Electronica 15, 1–134.

Millot, C., 1991. Mesoscale and seasonal variabilities of the circulation in the Western Mediterranean. Dyn. Atm. Oceans 15, 179–214.

Millot, C., 1999. Circulation in the Western Mediterranean Sea. J. Mar. Syst. 20, 423–442.

Mojtahid, M., Jorissen, F.J., Lansard, B., Fontanier, C., Bombled, B., Rabouille, C., 2009. Spatial distribution of live benthic foraminifera in the Rhône prodelta: faunal response to a continental-marine organic matter gradient. Mar. Micropalentol. 70, 177–200.

Murray, J.W., 2001. Ecology and Paleoecology of Benthic Foraminifera. Longman Scientifc & Technical, New York.

Murray, J.W., 2006. Ecology and Applications of Benthic Foraminifera. Cambridge University Press, Cambridge.

Nardelli, M.P., Jorissen, F.J., Pusceddu, A., Morigi, C., Dell'Anno, A., Danovaro, R., De Stigter, H.C., Negri, A., 2010. Living benthic foraminiferal assemblages along a latitudinal transect at 1000 m depth off the Portuguese margin. Micropaleontology 56 (3–4), 323–344.

Nardelli, M.P., Sabbatini, A., Bonnot, E., Mea, M., Pusceddu, A., Danovaro, R., Durrieu de Madron, X., Negri, A., Bicchi, E., 2018. Benthic foraminiferal assemblages in the Cap de Creus canyon and adjacent open slope: potential influence of dense shelf water cascading and open-ocean convention. Deep Sea Res (in press).

Nezlin, N.P., Lacroix, G., Kostianoy, A.G., Djenidi, S., 2004. Remotely sensed seasonal dynamics of phytoplankton in the Ligurian Sea in 1997–1999. J. Geophys. Res. 109, (C07013). https://doi.org/10.1029/2000JC000628.

Palmer, M.W., 1993. Putting things in even better order: the advantages of Canonical Correspondence Analysis. Ecology 74 (8), 2215–2230.

Papale, M., Conte, A., Del Core, M., Zito, E., Sprovieri, M., De Leo, F., Rizzo, C., Urzì, C., De Domenico, E., Luna, G.M., Michaud, L., Lo Giudice, A., 2018. Heavy-metal tolerant microorganisms in sediments from submarine canyons and the adjacent continental slope in the northeastern Ligurian margin (Western Mediterranean Sea). Progr. Oceanog. 168, 155–168.

Patterson, T., Fishbein, E., 1989. Re-examination of the statistical methods used to determine the number of points counts needed for micropaleontological quantitative research. J. Paleontol. 67, 475–486.

Phipps, M., Jorissen, F., Pusceddu, A., Bianchelli, S., Stigter, H.D., 2012. Live benthic foraminiferal faunas along a bathymetrical transect (282–4987 M) on the Portuguese Margin (ne Atlantic). J. Foraminif. Res. 42, 66–81.

Pierdomenico, M., Martorelli, E., Dominguez-Carriò, C., Gili, J.M., Chiocci, F.L., 2016. Seafloor characterization and benthic megafaunal distribution of an active submarine canyon and surrounding sectors: the case of Gioia Canyon (Southern Tyrrhenian Sea). J. Mar. Syst. 157, 101–117.

Pierdomenico, M., Gori, A., Guida, V.G., Gili, J.M., 2017. Megabenthic assemblages at the Hudson Canyon head (NW Atlantic margin): habitat-faunal relationships. Prog. Oceanog. 157, 12–26.

Pierdomenico, M., Cardone, F., Carluccio, A., Casalbore, D., Chiocci, F., Maiorano, P., D'Onghia, G., 2019. Megafauna distribution along active submarine canyons of the central Mediterranean: relationships with environmental variables. Prog. Oceanog. 171, 49–69.

Pusceddu, A., Dell'Anno, A., Fabiano, M., Danovaro, R., 2009. Quantity, biochemical composition and bioavailability of sediment organic matter as complementary signatures of benthic trophic status. Mar. Ecol. Prog. Ser. 375, 41–45.

Pusceddu, A., Bianchelli, S., Martín, J., Puig, P., Palanques, A., Masqué, P., Danovaro, R., 2014. Chronic and intensive bottom trawling impairs deep-sea biodiversity and ecosystem functioning. Proc. Nat. Acad. Sci. 111, 8861–8866.

Rathburn, A.E., Corliss, B.H., 1994. The ecology of living (stained) deep-sea benthic foraminifera from the Sulu Sea. Paleoceanography 9 (1), 87–150.

Romano, E., Bergamin, L., Finoia, M.G., Carboni, M.G., Ausili, A., Gabellini, M., 2008. Industrial pollution at Bagnoli (Naples, Italy): benthic foraminifera as a tool in integrated programs of environmental characterization. Marine Pollut. Bullet. 56, 439–457.

Rowe, G.T., Polloni, P.T., Haedrich, R.I., 1982. The deep-sea macrobenthos on the continental margin of the northwest Atlantic Ocean. Deep-Sea Res. 29 (2), 257–278.

Ruiz, F., Borrego, J., González-Regalado, M.L., López González, N., Carro, B., Abad, M., 2008. Impact of millennial mining activities on sediments and microfauna of the Tinto River estuary (SW Spain). Mar. Poll. Bull. 56, 1258–1264.

Sabbatini, A., Bonatto, S., Bianchelli, S., Pusceddu, A., Danovaro, R., Negri, A., 2012. J. Mar. Syst. 105, 163–174.

Savenkoff, C., Prieur, L., Reys, J.P., Lefevre, D., Dallot, S., Deni, S., 1993. Deep microbial communities evidenced in the Liguro-Provencal front by their ETS activity. Deep Sea Res. I 40, 709–725.

Schönfeld, J., 2002. Recent benthic foraminiferal assemblages in deep high-energy environments from the Gulf of Cadiz (Spain). Mar. Micropaleontol. 44, 141–162.

Schönfeld, J., Alve, E., Geslin, E., Jorissen, F., Korsun, S., Spezzaferri, S., Members of The Fobimo, 2012. The Fobimo (FOraminiferal BIo-MOnitoring) initiative—towards a standardized protocol for soft-bottom benthic foraminiferal monitoring studies. Mar. Micropaleontol. 94–95, 1–13.

Schmiedl, G., de Bovée, F., Buscail, R., Charrière, C., Hemleben, C., Medernach, L., Picon, P., 2000. Trophic control of benthic foraminiferal abundance and microhabitat in the bathyal Gulf of Lions, western Mediterranean Sea. Mar. Micropaleontol. 40 (3),

167–188.
Scott, D.B., Tobin, R., Williamson, M., Medioli, F.S., Latimer, J.S., Boothman, W.A., Asioli, A., Henry, V., 2005. Pollution monitoring in two North American estuaries: historical reconstructions using benthic foraminifera. J. Foramin. Res. 35, 65–82.
Sen Gupta, B., 2002. Modern Foraminifera. Kluwer Academic Publishers, The Netherlands.
Sen Gupta, B., Lobegeier, M., Smith, L., 2009. Foraminiferal Communites of bathyal Hydrocarbon seeps, northen Gulf of Mexico: a taxonomic, ecologic and geologic study. Coastal Marine Inst. 213, pp.
Sgarrella, F., Moncharmont-Zei, M., 1993. Benthic Foraminifera of the Gulf of Naples (Italy): systematics and autoecology. Boll. Soc. Paleontol. It. 32, 145–264.
Shepard, F.P., Dill, R.F., 1966. Submarine canyons and Other Sea Valleys. Rand, McNally, USA.
Snider, L.J., Burnett, B.R., Hessler, R.R., 1984. The composition and distribution of meiofauna and nanobiota in a central North Pacific deep-sea area. Deep-Sea Res. 31, 1225–1249.
Swallow, J.E., Culver, S.J., 1999. Living (Rose Bengal stained) benthic foraminifera from New Jersey continental margin canyons. J. Foramin. Res. 29 (2), 104–116.
Van der Zwaan, G.J., 1982. Paleoecology of Late Miocene foraminifera. Utrecht Micropaleontol. Bull. 25, 201 pp.
Van der Zwaan, G.J., Duijnstee, I.A.P., den Dulk, M., Ernst, S.R., Jannink, N.T., Kouwenhoven, T.J., 1999. Benthic foraminifers: proxies or problems? A review of paleocological concepts. Earth-Sci. Rev. 46, 213–236.
Van Oevelen, D., Soetaert, K., Garcia, R., de Stigter, H.C., Cunha, M.R., Pusceddu, A., Danovaro, R., 2011. Canyon conditions impact carbon flows in food webs of three sections of the Nazaré canyon. Deep-Sea Res. II 58, 2461–2476.
Vetter, E.W., Dayton, P.K., 1999. Organic enrichment by macrophyte detritus, and abundance patterns of megafaunal populations in submarine canyons. Mar. Ecol. Prog. Series 186, 137–148.
Vetter, E.W., Smith, C.R., De Leo, F.C., 2010. Hawaian hotspots: enhanced megafaunal abundance and diversity in submarine canyons on the oceanic islands of Hawaii. Mar. Ecol. 31 (1), 183–199.
Walton, W.R., 1952. Techniques for recognition of living foraminifera. Contributions from the Cushman Found. Foramin. Res. 3, 56–60.